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CALVING AND RELATED SOCIAL BEHAVIOR
IN THE BARREN-GROUND CARIBOU

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled Calving and Related Social Behavior in the Barren-Ground Caribou submitted by Peter Charles Lent in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

Some aspects of the behavior of the barren-ground caribou (Rangifer tarandus groenlandicus) were studied during four seasons of observation in northwest Alaska. Particular emphasis was placed on the calving season and on mother-infant relationships.

Ninety per cent of the calves were born in 2 weeks at the end of May and in early June. The proportion of cows with calves at the end of this calving period was 73 per cent in 1960 and 42 in 1961. Almost no adult males and only about 40 per cent of the yearlings entered the calving area. The calving ground is the most invariable point in the migratory pattern of caribou and appears to be traditionally determined. Calving groups are entirely open. Coalescence of groups begins at the calving peak and results in a constant increase in the size of groups until early July. Cows with calves tend to move together ("nursery bands") and yearlings tend to occur in groups with barren cows, but near the end of calving all individuals, including adult males, begin to mix together.

Cows may give birth while in groups or alone but usually do not seek isolation before parturition. The neonate stands within half an hour after birth and is soon walking. The first nursing may be delayed until the second hour or later. The mother must actively maintain the bond with her infant, at first by frequent physical contact; later by acts eliciting following (head bobbing, grunting, and attraction pose), by agonistic acts towards other cows and calves, and by searching for her infant if separation occurs.

Head bobbing is a behavior pattern of widespread importance in caribou. It is probably a displacement activity derived from the feeding motion. Ritualized head bobbing is a strong releaser of approach responses in calves and shows qualities similar to experimentally produced stimuli eliciting such responses in young birds.

Some aspects of the calves' early behavior are considered as simple responses to stimuli of optimum intensity. Social play is not developed but exploratory behavior among young calves is common and its importance in learning is suggested.

Nursing is either from the side or from between the hind legs. It is more often successful and of longer duration when performed from the side. The mean duration of each nursing (31 sec) does not vary with age but frequency (ca. once every 18 min in first 2 days) decreases after the first week.

Five types of agonistic acts occur. One ("antler threat") is directed by cows primarily towards calves. Outside of the rut actual contact in agonistic events is rare, as are acts of reciprocation. The high degree of tolerance is related to the early social experiences of the calf. Cows with calves dominate other cows and all cows dominate yearlings.

Responses to strange, disturbing stimuli vary greatly according to a variety of factors. Cows with young calves show special responses. When temporarily abandoned by their mothers, infants may remain motionless when approached by a man but may also follow him after being handled.

Similarities are apparent in the behavior of caribou and their ecological equivalents of the African grasslands, the wildebeest and Thomson's gazelle. The more pronounced peak in breeding activity in caribou accounts for many of the differences.

ACKNOWLEDGEMENTS

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In 1962 I was able to continue my study with a grant from the Arctic Institute of North America (under contractual agreement with the U.S. Office of Naval Research) and in 1962 and 1963 additional field work was made possible by a grant from the U.S. National Science Foundation to Dr. Wm. A. Fuller. In addition, since 1962 I have been supported by National Science Foundation Graduate Fellowships.

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I. INTRODUCTION

If we accept the interpretation of Bourliere (1960: 156) of a Paleolithic cave drawing showing a male and female reindeer (Rangifer tarandus), it appears that the behavior of reindeer has been attracting the attention of men for some thousands of years. In spite of this, and in spite of the fact that the reindeer has served man as a domestic animal for perhaps as long as 4,000 years (see Manker, 1954 and Bosi, 1960), there has been little systematic examination of its behavior until very recently.

In 1931, Jacobi summarized all that was known about the species at that time in his monograph in German. Soon after (1935), Murie's publication on the caribou of Alaska appeared, containing a surprising amount of accurate information on natural history, considering the means available for studying caribou at that time.

Also during the thirties a vast amount of research was carried out in the U.S.S.R. with domestic reindeer. This work was all of a practical nature, dealing with such subjects as breeding, forage, parasites and utilization. One Russian paper appearing in this period, that of Sdobnikov (1935), has become the most widely quoted source of information on reindeer social behavior; cited in such texts as Allee et al. (1949) and Roe and Simpson (1958) as well as in the more recent monograph on reindeer by Herre (1955). However, there has been no confirmation of the ideas set forth by Sdobnikov

in any work since then and there is little reference to his paper in the recent Soviet literature.

Some similar applied research with domestic reindeer was carried out in Alaska during the twenties and thirties by the Bureau of Biological Survey. Since then, reindeer management and research in North America has stagnated.

The first modern studies of the barren-ground caribou were made possible by the increased availability of airplanes for the use of biologists in the post-war decade. The first such study was done in Canada by Banfield (1954) and was later continued under the direction of Kelsall (1957, 1960). From these cooperative investigations of the barren-ground caribou by the Canadian Department of Northern Affairs and National Resources and the provinces of Manitoba, Alberta and Saskatchewan have come two papers dealing specifically with the behavior of caribou (de Vos, 1960; Pruitt, 1960).

During the past decade similar research with caribou has been carried out in Alaska, first by the U.S. Fish and Wildlife Service, and more recently by the Alaska Department of Fish and Game. The primary emphasis in both the Canadian and Alaskan work has been on population phenomena, movements and, to a lesser extent, range and feeding habits. Since very little of the results of these investigations has been made available in widely read zoological journals, I have attempted to examine these results as thoroughly as possible and include all pertinent behavioral data here.

The basic goal of my study was to add as much as possible to the existing knowledge of social behavior in the barren-ground caribou, particularly as it relates to calving and the migratory habit. During the early stages of my ecological investigations of the caribou in northwest Alaska, my attention was attracted to the problem of the care and development of the infant in such a highly mobile, gregarious, migratory species. Thus the mother-infant relationship forms the central theme of this thesis. I have attempted not only to describe the behavior patterns operating in this relationship but also to compare them with those occurring in other ungulates, both migratory and non-migratory, to obtain a better understanding of the survival value of such patterns. Other social and, to a lesser extent, ecologic factors affecting the mother and infant are considered.

II. METHODS

Field observations and aerial survey work were carried out throughout 1960, except from late August to mid-September, and continued in 1961 until mid-July. I returned to the study area to observe rutting behavior in late October and early November of 1961. An additional 3 months were spent in the field in 1962 and 1963.

Observations of behavior relating to calving and the periods before and after calving were made during the 4 years, 1960 through 1963, between the following dates.

1960: May 27 - August 27

1961: May 15 - July 12

1962: May 21 - July 4

1963: May 10 - June 23

No detailed, quantitative records of social behavior were made during 1960. Aerial observations and a calf tagging program (see Lent, 1961) were the principal activities during this first calving season. Much time was also spent watching general behavior and the reactions of animals to man in order to be able to distinguish between disturbed and undisturbed individuals. All the statistics presented regarding behavior are based on the last 3 years of field work.

Observations of rutting and winter behavior made in 1960 and 1961 are not reported here except for some material relevant to the topics discussed.

It is impossible to state how many hours of actual

observation were made in the entire study. Whenever possible, I have stated the number of observations on which a certain description or conclusion is based. These numbers refer only to observations made during periods when behavior was being systematically recorded, and not to chance observations made during the course of other activities, such as counting and specimen collecting.

During calving, when the caribou are particularly wary, there were many days when more hours were spent hiking towards and stalking caribou groups than were spent in actual observation. The use of a 20 power spotting scope was necessary on most occasions during this period. The disadvantage of observations made at a distance is that vocal signals cannot be heard. However, enough close observations were made to gain an adequate picture of the role played by vocalizations. The use of vocal signals was frequently noticed visually through the spotting scope. Outside of the actual calving period most observations could be made with binoculars (7 x 50) or with the unaided eye.

On sunny days during the calving season observations with the spotting scope were limited to the late afternoon and early evening hours because of the severity of atmospheric heat-wave distortion in the morning hours. On cloudy days this distortion was not as pronounced. In late June and early July observations could be made during all hours and a more even distribution of observation periods was obtained.

Most observations were recorded on a small tape

recorder. This procedure permitted the recording of detailed descriptions without taking any attention away from the subject.

Each observation in the transcriptions from the tape recordings and in my field notes, as well as those of my assistants, was then catalogued on a punch card and classified according to time of year of the observation, class of individual(s) involved and the nature of the event or interaction. This system ensured consideration of all observations bearing on each aspect of the study. Statistical methods outlined in Simpson et al. (1960) were followed.

On many occasions when caribou were easily accessible from campsites their behavior was recorded with a 16 mm motion picture camera. Approximately 3,000 feet of film were taken and examined. Out of this, about 800 feet were used to produce a half-hour research film entitled, "The Behavior of the Barren-Ground Caribou". A copy of this film is on file at the University of Alberta and another copy is in the possession of the author. In Appendix A of this thesis the behavior patterns shown in the scenes in the film relating to calving and postcalving behavior are listed with descriptive notes. References to these scenes are made where appropriate throughout the text of the thesis. It is hoped that in this way both the film and the thesis will be of greater value for other research workers. In addition to the film footage many 35 mm still pictures were taken, some of which are shown in the text.

The use of small, "bush" aircraft was essential for a study of this nature, not only for counting the caribou and

plotting their movements, but also for moving camps to locations where a large number of animals was accessible for observation.

In spite of the aid of modern aircraft the greatest difficulty in the study was the inability to maintain continuous observations on the same individuals. By the second day after parturition mothers and their infants may be traveling 10 or more miles per day over rough terrain and across rivers. It was thus impossible to follow individuals on foot. Older calves, traveling rapidly during the post-calving movement, could be observed for only a few hours at best. Only by the use of a helicopter could one possibly maintain continuous contact with such migratory individuals. Unfortunately, the use of helicopters is still beyond the financial limitations of most game biology research. Observations and experiments with reindeer or captive caribou would add a large amount of information not obtainable from the study I have carried out.

I was able to observe two calves on 3 consecutive days, including the day of birth, and three others were observed on 2 consecutive days. Ten other calves for which the time of birth was known were watched for periods of up to 5 hours after birth. Additional information was obtained by McWilliams in 1960 during the tagging of calves (Lent, 1961), particularly from one calf tagged soon after birth and then mistakenly recaptured later during its first day.

The development of these neonate calves of known age was watched closely. These observations were then used

as a basis for estimating the age of other young calves.

It was clear that the development of these known-age calves in the hours following their birth was variable. This variability in motor development was also evident in the differences between individuals in post-partum activity, as described in Section 6. In general, however, something close to the following sequence of development was observed.

First half-hour: The calf may stand briefly but loses balance and collapses quickly.

Second half-hour: All calves are able to stand; some are moving a few yards at a time but lose their balance often. The hind legs are curved inwards, pointing towards one another at the hock joints, and are bent sharply. The feet are placed far apart and the body sways from side to side when the calf stands or moves (Fig. 1).

One to four hours: The calf is able to follow at a walking gait for at least a few yards or even up to a mile, depending upon the individual. The hind legs are still sharply bent with the tibia parallel to the ground. The calf loses balance occasionally but placement of the feet appears more certain and swaying is decreased. The back appears hunched and the neck dips sharply (Fig. 2).

Four to six hours: All calves are able to follow the mother for long distances. A few are still limited in speed to about that of a fast-walking man. The tibia is held more diagonally to the ground and the hunched appearance is gone or nearly gone.



Fig. 1. Calf under 1 hour old.



Fig. 2. Calf about 2 hours old.

Six to twenty-four hours: Calves are running and trotting. They show a bounding gait when moving fast. The hind legs remain conspicuously bent.

Second day: Two out of three known-age calves showed almost completely straightened hind legs and were able to maintain their mother's running pace for a long distance. They were able to swim across streams. The third calf still showed a bouncy, awkward gait and noticeable bending of the hind legs.

Third day: The calves showed few of the characteristics of younger calves, and were able to run as fast as or faster than the mother, but still tired sooner. The gait at this age appeared quite graceful (Fig. 3).

After the first few days the ages of calves could be estimated only on the basis of visual weight estimates, pelage changes and antler growth. In addition, statistics on the start, peak and end of calving were helpful in estimating the minimum, maximum and mean ages of calves observed in postcalving groups.

During the first week of July the oldest calves (5 to 6 weeks old) show longer, lighter-colored hair appearing in the pelage and their pelts lose their primeness. Antler growth also commences and visible bony nobs form in late July. By winter the males have spikes of 8 to 12 inches, the females have somewhat shorter spikes (see Banfield, 1954).



Fig. 3. Calf about 1 week old.



Fig. 4. Nursery band in Eriophorum tussock community. June 5, 1960.

III. THE STUDY POPULATION

Present Range

At the time of its maximum dispersal in winter the study population is spread over an area of approximately 85,000 square miles. Most of this range lies north of the Arctic Circle (Fig. 5).

The area varies from true boreal forest on its southern boundary to low, wet coastal tundra on the north, bordering the Arctic Ocean. It is completely divided into a north and a south section by the western end of the Brooks Range, including the De Long Mountains, Baird Mountains and Schvatka Mountains, the latter being the highest with some peaks between 8,000 and 9,000 feet. Most of the higher peaks in the De Long and Baird Mountains are between 4,000 and 5,000 feet.

That part of the range lying north of the crest of these mountains lies within the region known as the Arctic Slope. This region is divided into three major physiographic provinces: the Coastal Plain, the Foothills and the Mountains (Spetzman, 1959). The calving area, which lies within the Foothills Province of the Arctic Slope (Fig. 5), will be described further in the section dealing with calving in the study population.

To give some picture of the climatic conditions in the study area, a summary of climatic data for two stations in the Arctic Slope region is shown in Fig. 6 (reproduced

Fig. 5
Overleaf

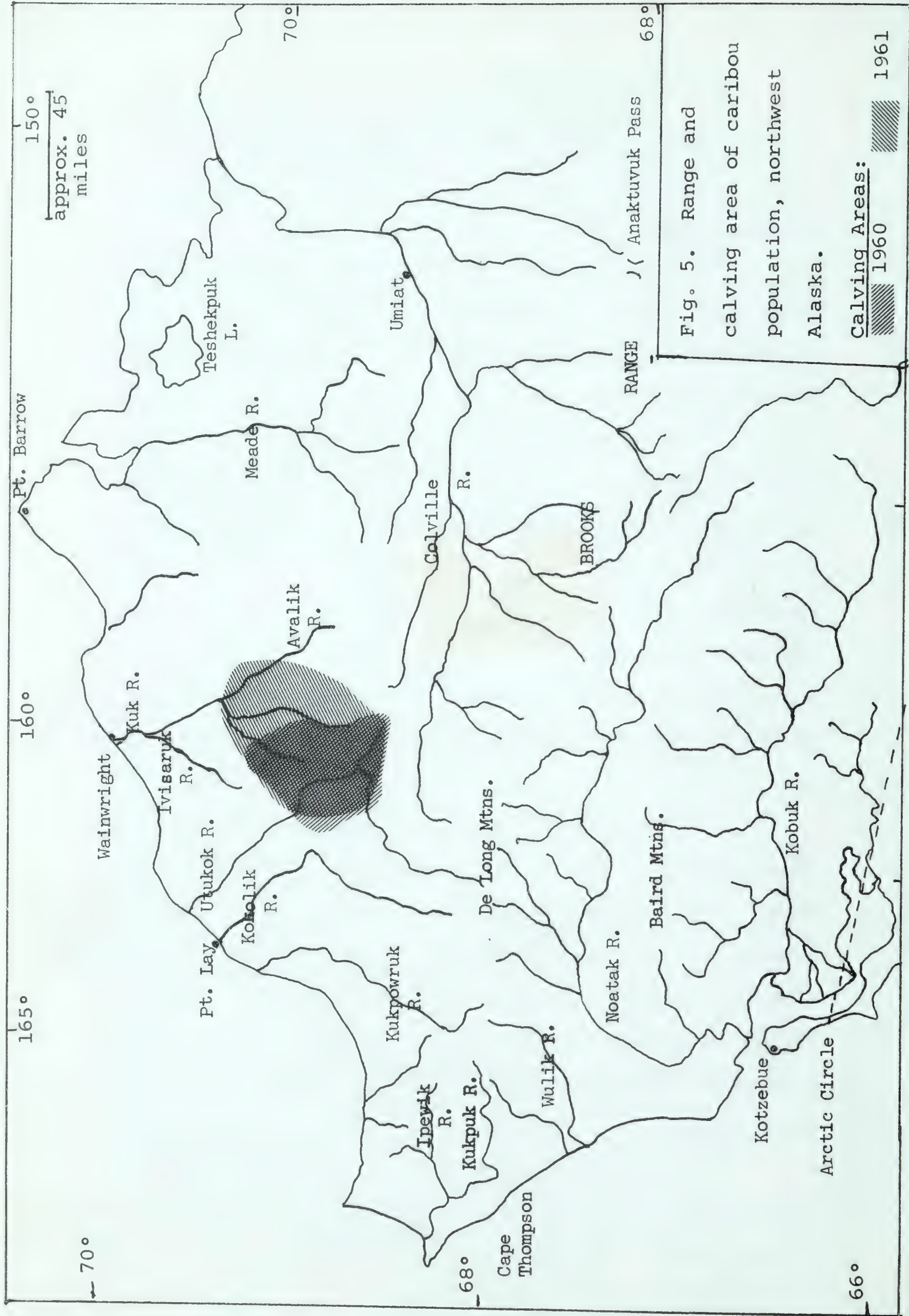


Fig. 5. Range and calving area of caribou population, northwest Alaska.

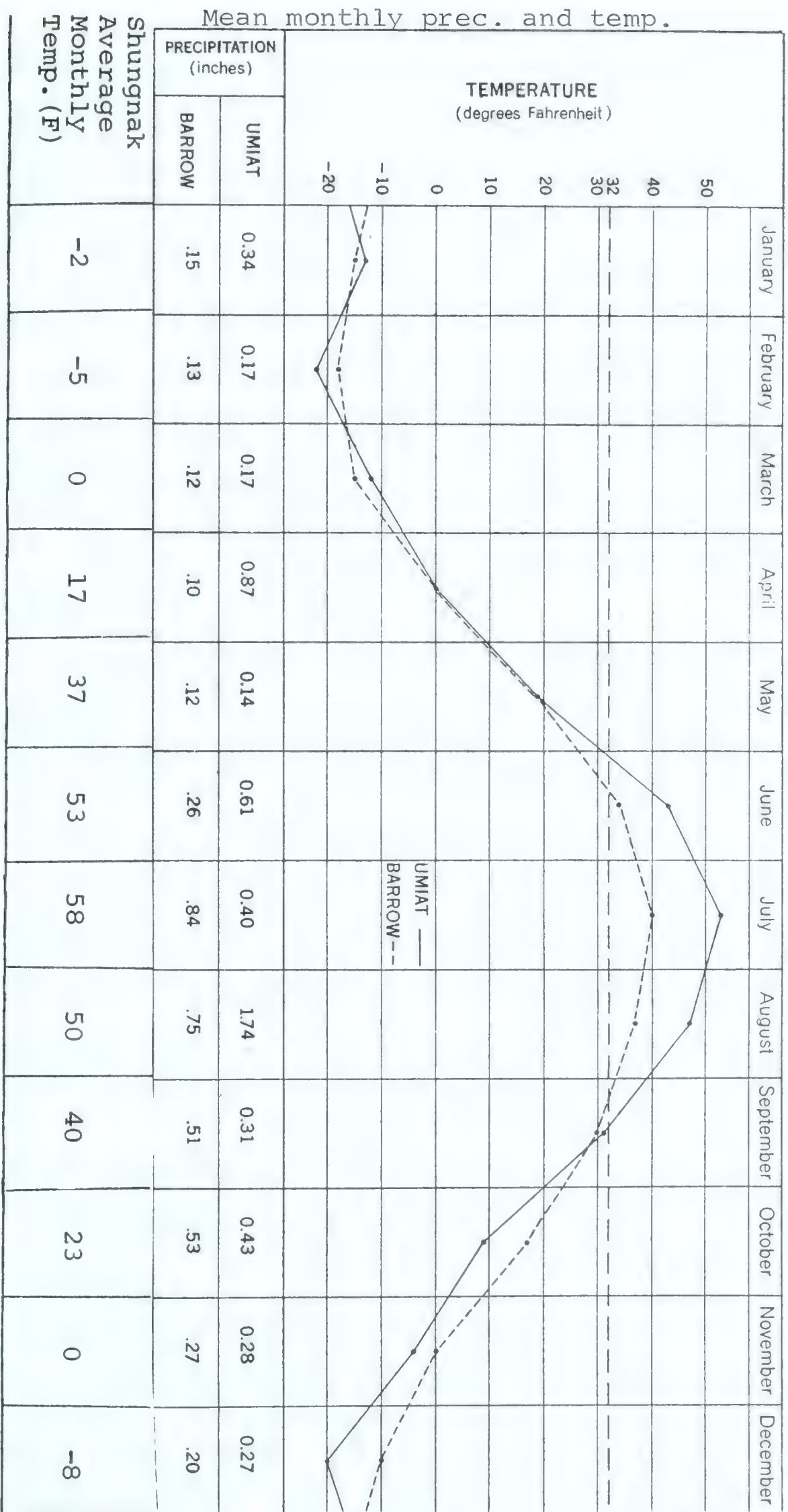


Fig. 6. Climatic data for two Arctic Slope Stations (reproduced from Spetzman, 1959)

with average monthly temperatures from Shungnak, a taiga station, shown for

comparison. Barrow: 29 year record, Umiat: 3 year record, Shungnak:

7 year record.

from Spetzman, 1959). At the bottom of Fig. 6, I have added average monthly temperatures for Shungnak, a station on the south slope of the Baird Mountains and on the northern edge of the taiga.

Taxonomy

The caribou population of northwestern Alaska had received only sporadic attention before the start of the Bioenvironmental Studies of Project Chariot. The principal published sources of information are Bailey and Hendee (1926), Murie (1935) and Bee and Hall (1956).

Lydekker (1898) considered that all members of the genus Rangifer are of the same species and most recent workers (see Flerov, 1960; Banfield, 1962) place all living members of the genus in the species Rangifer tarandus. At the sub-species level, however, the taxonomy of the study population remains uncertain. Banfield, the most recent worker to deal with the subject, leaves the question unsettled, but states that specimens from the Brooks Range could not be separated adequately from R. tarandus groenlandicus, the "tundra reindeer" of the Canadian barrens.

One problem which Banfield recognized in his taxonomic consideration of Alaskan caribou is that of the introduction of Siberian reindeer into many areas. Although the peak of the breeding season in these introduced Siberian reindeer occurs about 1 month earlier than that of the Alaskan caribou (see Table 9), this difference does not prevent interbreeding (Murie, 1935). Since the reindeer is seasonally

polyestrous (Gorbunov, 1939), it seems likely that reindeer females not fertilized during their first heat would be mated in later estrous periods.

At present there is no good evidence indicating to what extent, if at all, the caribou population of northwest Alaska has been modified by interbreeding with introduced reindeer. Since this aspect has not been adequately studied, the possibility exists that the behavior of the study population may have been modified slightly by the genetic influences of reindeer stock.

History

Starting in the mid-nineteenth century, after the encroachment of the European upon the domain of the Eskimo, there was a rapid decrease in the number of caribou in western Alaska. This decrease was first noted in the lower Yukon River drainage where the influence of Russian exploration was first felt. At the time of the early Russian explorations, caribou were plentiful throughout this area, and in 1867, for example, Dall (1870) reported seeing over 4,000 "reindeer" calf skins at Anvik on the Yukon River. By 1878 they were almost non-existent in this same area according to Nelson (1887:285) who described the change as follows:

When the American Telegraph explorers visited Alaska in 1866-67, reindeer [caribou] were found everywhere and herds containing thousands of individuals were no uncommon sight. They were very abundant on the hills and valleys bordering upon Norton Sound, but today their

former abundance is indicated only by the number of antlers scattered over the country and the well marked trails worn on the hillsides or leading across the valleys ...

Nelson goes on to describe the almost complete absence of caribou in the vicinity of Saint Michaels where he lived and explored for three years (1878-1881) without ever seeing one. He states that caribou were at that time still plentiful at the head of the Kobuk River and on the barrens stretching to the Arctic Ocean. He predicted that these would very soon be as scarce as elsewhere because of indiscriminate hunting. According to him, "In the summer of 1880 one man from Point Barrow took about 500 skins and many others took nearly as large a number" (Nelson, 1887:285).

In 1878 caribou were becoming increasingly scarce along the northwest coast so that Eskimos were making hunting trips to Nunivak Island and soon exterminated the population there (Murie, 1935). By the 1890's caribou had become scarce over the entire coast, at least as far as Barrow (Jackson, 1897).

Several observers during this period indicated that the decrease was first noticeable along the west and north coasts, later progressing inland and to the east (see Murie, 1935). This description would be logical, for all European influences were felt most strongly along the coast and in the west, but the observations cited by Murie implied that there were resident populations of caribou along the coast separate

from those inland. This concept does not fit the present day movements, and it is doubtful if there would have been resident groups within the larger population.

Bee and Hall (1956) suggest that the decline of the caribou population in northern Alaska was due in large part to the introduction of reindeer. This suggestion appears to have no basis in fact. The decrease in caribou was under way long before even the first few reindeer were introduced in 1892. In fact, the scarcity of caribou was one of the reasons given by Jackson (1894) for the introduction of reindeer. Changes in the hunting technology of Eskimos brought about by the introduction of the rifle and the demands of overwintering whaling crews for fresh meat are given as reasons for the decrease in caribou numbers by Sonnenfeld (1960).

Observers first noted a gradual increase in caribou abundance in northern Alaska in the early 1920's (Bailey and Hendee, 1926; Murie, 1935). The end of the whaling era and the decrease in the numbers of Eskimos undoubtedly aided the recovery of the caribou population. In addition, most of the surviving inland Eskimos had by this time moved to the coast and were no longer as dependent upon caribou for survival.

The total number of domestic reindeer in Alaska reached a peak estimated at more than 600,000 in 1932 and subsequently dropped sharply to about 25,000 in 1950 (Sonnenfeld, 1959). Thus the increase in the number of caribou began before the number of reindeer reached its maximum and continued concurrently with the decrease in reindeer. In fact,

the influence of increasing numbers of migrating caribou is frequently given as one of the reasons for the decline in reindeer (Lantis, 1950; Sonnenfeld, 1959). Even at its peak reindeer herding appears to have exerted little influence on the caribou. The land overgrazed by reindeer was negligible compared to the overall range available to the migratory caribou.

One region which appeared to be only partially affected during the drop in caribou numbers lay just north of the Brooks Range on the upper Colville River, and from the Killik River to the Utukok River. Schraeder (1904) reported caribou to be plentiful in this region even though they were apparently scarce along the adjacent coast in the same years (ca. 1901).

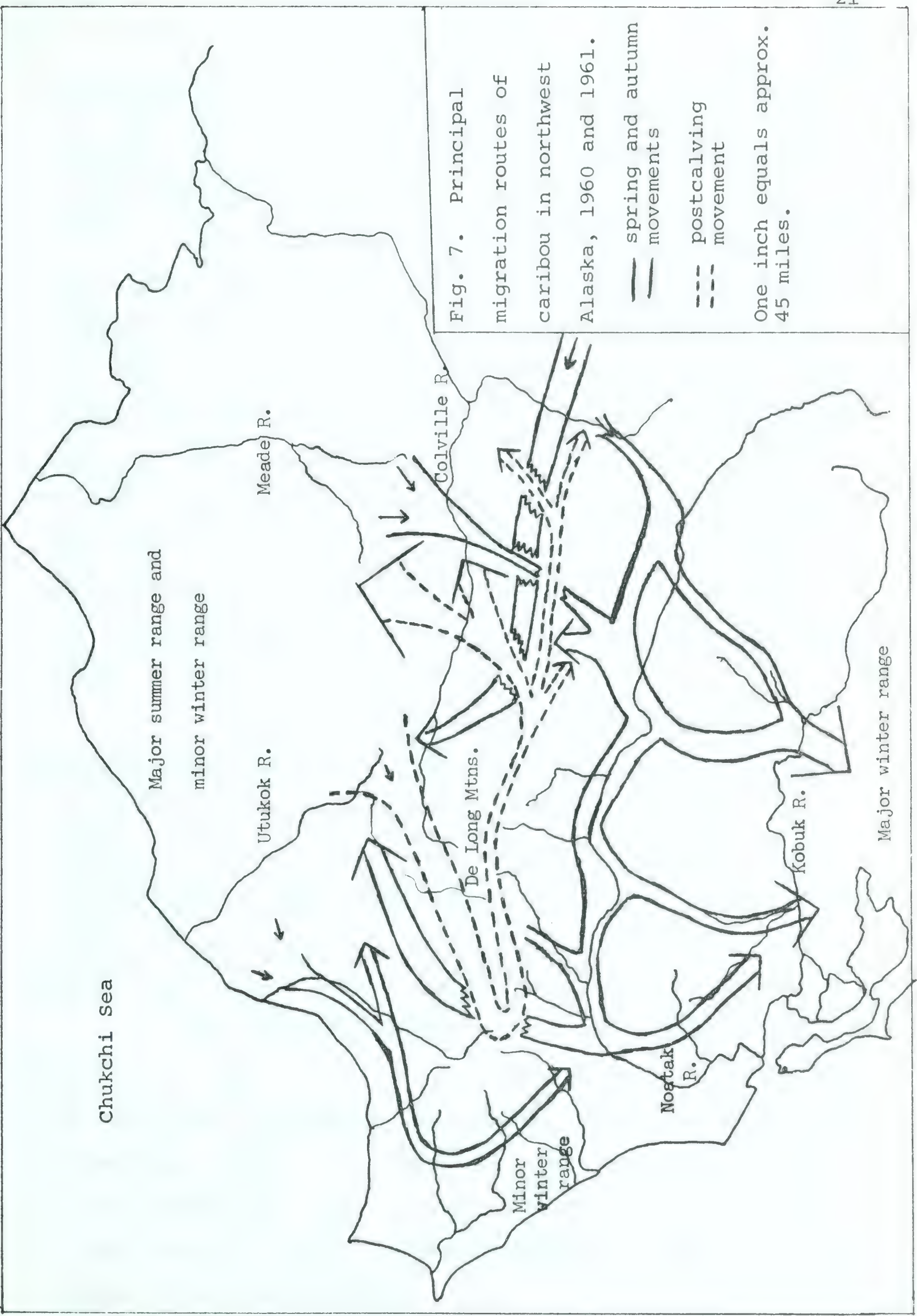
Samuel Agnassaga, of Point Lay (pers. comm., 1961) reports that caribou calved in the general region of the upper Utukok River when he was a boy (ca. 1910-1915). The Utukokmiut (people of the Utukok River) were perhaps the largest group of inland Eskimos north of the Brooks Range before the arrival of the European (Spencer, 1959, and Agnassaga, pers. comm.). These people came down to the coast in the summer to trade caribou calf skins, among other things. Murie (1935:65) describes how in more recent times, "... natives from Point Lay, Icy Cape and Wainwright came up the Utukok and also portaged over the Kuk to get caribou on the upper Utukok." The observations summarized by Murie indicate that even when the caribou population of the Arctic Slope was at its lowest point, the Utukok River drainage and the upper Colville River area continued to be a center of relative abundance.

Size, Composition and Recruitment

A difficult problem encountered during the investigation was how to determine accurately the size of the population. This problem was never entirely solved, however an approximate figure was obtained.

During the late summer, fall, and winter months when the population was dispersed over its entire range transect counts to accurately determine caribou densities in all areas were impossible, both because of financial limitations and because of the lack of satisfactory flying weather on a sufficient number of consecutive days to accomplish a survey. At the time of the precalving movement, when snow melting had occurred to expose tussock tops, snow conditions on the tundra and in the hills produced a speckled background against which caribou were difficult to see. Cows could have been counted during the calving time, but the press of other phases of the study during the days of good weather eliminated this possibility.

The best time to obtain a count of the population appeared to be at the time of maximum concentration during the last week of June. At this time all snow cover was gone but the caribou still retained most of their old, light-colored pelage, making them stand out well against the dark background of low vegetation and rocks. In 1960, 1961 and 1962, almost the entire population formed into two or three large masses at the point where the population turned East in the postcalving movement (Fig. 7). Since the individuals



were too densely packed in these masses to permit counting directly from the airplane, aerial photography appeared to be the only solution.

On June 28, 1961, aerial photos were taken using a K-24 camera installed in a Cessna 195 supplied by the Arctic Research Laboratory, Barrow. Not all the photos were usable, but counts were made directly from about 100 negatives. These counts were compared with visual estimates of the same groups. The comparisons showed that visual estimates of groups over 15,000 averaged 30 per cent higher than the actual number on the negatives. Applying the 30 per cent correction factor to my estimates of groups not satisfactorily photographed, a total observed population of 130,000, plus approximately 25,000 calves of the year, was calculated.

In 1962 another aerial photography flight was planned but proved impossible because of bad weather during the few days before the population dispersed into the mountains. Corrected visual estimates indicated that some small segments of the population may have been missed in 1961 and it appears likely that the 1962 summer population was between 175,000 and 200,000 including calves.

The approximate composition of the population as it existed in early July of 1961 is shown in Table 1. The sample was taken from aggregations of animals representing more than 90 per cent of the total population. All samples taken during the rutting season showed a somewhat lower proportion of adult males. "Adult" is used throughout to refer to all animals older than yearlings.

Table I. Proportion of cows, bulls, yearlings and calves in study population, July, 1961.

Class	Number segregated	Per cent of adults	Per cent (excl. calves)	Per cent of total population (incl. calves)
Cows	1,179	55	46	38
Bulls	959	45	37	31
Yearlings	440	--	17	14
Calves	<u>495</u>	<u>--</u>	<u>--</u>	<u>16</u>
TOTAL:	3,073	100	100	99

The number of calves per 100 cows in the aggregations after calving varied considerably in the three years 1960, 1961 and 1962, being 73, 42, and 53, respectively. In 1961 and 1962 the number of yearlings per 100 cows in these aggregations was 37 and 22. Thus about half of the calves alive at the end of the calving season survived to the age of 13 months (Table 2).

Pattern of Migration

The major precalving, postcalving and autumnal movements of the northwest Alaska caribou population as they were observed in 1960 and 1961 are shown in Fig. 7.

Striking changes in the structure of the snow cover and the proportion of ground covered with snow were observed in April of both years, particularly in the mountains and in the foothills on both slopes of the Brooks Range. A rapid northward movement in April and May brought most of the cows

Table 2. Proportion of calves and yearlings to cows in the calving and postcalving periods, 1960, 1961 and 1962.

		<u>Samples</u>	
		<u>1960</u>	
		<u>cows</u>	<u>calves</u>
Per cent of cows with calves at end of calving period	73%	2,300	1,680
		<u>1961</u>	
		<u>cows</u>	<u>yearlings</u>
Number of yearlings per 100 cows in central calving area	15	244	37
Number of yearlings per 100 cows in postcalving period*	37	1,180	440
		<u>cows</u>	<u>calves</u>
Per cent of cows with calves at end of calving period	42%	17,000	7,140
		<u>1962</u>	
		<u>cows</u>	<u>yearlings</u>
Number of yearlings per 100 cows in central calving area	9.5	357	34
Number of yearlings per 100 cows in postcalving period*	22	2,899	630

* Last week of June and first week of July.

to the dry-tundra calving grounds in the foothills of the Arctic Slope (Fig. 5) at the same time as most of the snow disappeared and the first green shoots and buds of cotton-grass (Eriophorum vaginatum) appeared. The calves were born in late May and the first half of June.

In late June and early July, after calving, the population was concentrated in the foothills and mountains where the willows, birches and forbs first yielded a wealth of new growth.¹ Soon after this most of the population dispersed onto the coastal tundra where the new growth of sedges and willows was finally beginning to develop.

In late August and early September, as the tundra vegetation withered and the first snow fell, the population again moved towards the South. In winter most of the population settled in the northern edges of the taiga but other, more dispersed, segments of the population spent the winter in the most wind-swept regions of the coastal tundra and foothills. Only an occasional small band of individuals was seen in the calving grounds during the fall and winter months. Animals that wintered in the taiga crossed through the mountains of the Brooks Range, many of them traveling 300 miles or more each way in their spring and autumn movements.

More detailed descriptions of movements by the study population may be found in Lent (1961, 1964) and in a summary by the U.S. Atomic Energy Commission (1962).

¹Spetzman (1959) describes the earlier and more favorable conditions for plant growth in the foothills in comparison to the tundra closer to the coast.

IV. CALVING IN THE STUDY POPULATION

Phenology of Calving

As in all known populations of caribou, there is a restricted period in the spring when almost all the calves of the study population are born. The dates for the start, peak and end of this period for the years 1960, 1961 and 1962 are shown in Table 3.

For purposes of this table, the three dates are defined as follows. The start of the calving season is the first day on which newborn calves were seen on the calving grounds. The peak date is the day by which half the calves were born. The calving season was considered at an end when no further increase in the proportion of cows with calves could be measured. Clearly all these dates are subject to some variation introduced by factors other than the actual number of calves born on each day, such as the extent of calf mortality, and the differences in the size of the samples taken in different years.

An occasional newborn calf was observed as late as July 4. No unusually early births were observed, however. That is, there was no gap between the day on which the first newborn calf was observed and the days on which subsequent observations of neonate calves were made.

The Calving Environment

I have already mentioned that the mass of pregnant cows in the population arrives in late May at an area in the

Table 3. Calving period of caribou in northwest Alaska,
1960, 1961 and 1962.

Year	Start	Peak	End
1960	May 22	May 26	June 5
1961	May 25	June 5	June 15
1962	May 29	--	June 13

Table 4. Summary of weather conditions on calving grounds.

	Utukok River area May 24 - June 21			Canadian Arctic, Beverley Lake, N.W.T. June. (Kelsall, 1960).		
	1961	1962	1963*	1948	1957	1958
Mean daily minimum temp. (F)	34.0	33.3	ca.37	37.9	31.6	27.6
Mean daily maximum temp. (F)	49.0	52.4	50	61.7	48.3	42.7
Mean wind velocity (mph)	6.4	8.3	--	6.7	13.2	11.3
Mean wind chill factor	635	781	--	640	907	893
No. days wind chill factor 1000 or more	4	1	1-3**	2	16	12

* May 24 - June 11 only

** Based on estimated wind velocities

foothills of the Arctic Slope where the budding of Eriophorum vaginatum is just beginning. This area, where almost all of the calves in the study population are born, is referred to as the "Utukok River calving area". The exact boundaries of the area vary from year to year. In Fig. 5 they are shown as they existed in 1960 and 1961.

No detailed vegetation studies have been carried out within the calving grounds. Spetzman (1959), however, described the vegetation at Umiat and Noluck Lake, locations also lying within the Foothills Province of the Arctic Slope. The predominant plant species is Eriophorum vaginatum but in poorly drained areas sedges (Carex spp.) are dominant; and along the ridges, especially above 1,500 feet elevation, avens (Dryas octopetala) and lichens are most common.

Calving takes place primarily in the low, rolling hills between 500 and 1,000 feet in elevation. Here, in 1960 and 1961 snow covered less than 20 per cent of the ground surface by the start of calving. At the same time in regions to the north and east of the calving area, the estimated proportion of ground surface covered with snow ranged from 50 to 90 per cent and to the south from 30 to 80 per cent. Within the calving area the rocky, snow-covered ridges over 1,500 feet are avoided until near the end of the calving season.

In Fig. 6 it may be noted that the average monthly temperature at Umiat, in the foothills, shows the greatest increase between May and June. A similar marked increase in

daily temperatures was observed in the calving area in 1960 through 1963. In the first 2 years and in 1963 the increase was evident by the last week of May but in 1962 it was delayed until the second week of June.

Daily weather records kept in 1961 and 1962 are shown in Appendix B. A summary of these records, together with some incomplete information on the 1963 season, appears in Table 4 and weather summaries given by Kelsall (1960) for Canadian Arctic calving grounds are shown for comparison. The averages of the estimated daily wind chill factors are also shown in Table 4. Wind chill factor is a measure of the cooling effect of the weather on man based on both air temperature and wind velocity. Some difficulties in the use of this measurement with regard to caribou are discussed by Kelsall (1960), who concludes that it provides a crude indicator of the weather conditions that might lead to calf mortality.

Although complete weather records were not kept for the Utukok River calving area in either 1960 or 1963, the conditions during these two calving periods were comparable to those of 1961.

Phenology of Antler Shedding by Adult Females

In 1961 particular attention was paid to the shedding of antlers by adult females on the calving grounds. To understand the reason for examining this phenomenon some reference to previous literature on the subject is necessary.

Many previous writers have noted that barren female

reindeer and caribou will drop their antlers before the start of the calving period and that bearing cows will usually retain their old antlers until after giving birth (Hadwen and Palmer, 1922; Popov, 1935; Skoog, 1957, 1959; de Vos, 1960, and Semenov-Tyan-Shanskii, cited in Flerov, 1960).

None of the above workers, however, have presented any detailed evidence to support this observation. Skoog (1959) does show that in 4 years observations on the "Steese Herd" of Interior Alaska the proportion of cows with antlers at the start of calving never differed by more than 3 per cent from the proportion of cows with calves at the end of calving.

In every Rangifer population there is a small number of adult females in any year that do not grow antlers at all (Herre, 1955). A sample of 1,099 cows observed during the rut in 1961 showed that approximately 3 per cent of the cows in the study population were without antlers at that time.

In the study population, 2,080 cows were observed in the calving area between May 16 and May 24, 1961. Of these cows, 53 per cent (1,107) had old antlers. This proportion is identical with the proportion of cows on the central calving grounds that were accompanied by calves at the end of the calving season (5,032 out of 9,428 = 53.3 per cent). This latter figure is based on counts made before most of the barren cows from the periphery of the calving area mixed in with the central calving segment. As was shown in Table 2, the proportion of cows with calves after this mixing (and after additional calf mortality) was 42 per cent.

Between May 28 and June 20 an additional 13,396 cows were observed and divided into two categories: those with calves and those without calves. Each of these categories was further divided into those with antlers and those without antlers. "With antlers" refers to cows with old, hard antlers as opposed to the new antlers in velvet that begin to grow soon after the shedding of these old ones.

The proportion of cows with antlers in each of the categories was calculated for each day on which samples were obtained. These proportions are plotted in Fig. 8. Except where noted only daily samples of more than 200 cows were used to plot the points on each line. It may be seen that the proportion of antlered cows was higher in the cows-with-calves category (line A) on every day. The data used for plotting six of the points on the graph are shown in Table 5. On four of the dates the difference between the proportion of antlered cows in the with-calf category is significantly higher ($P < .05$) than the proportion antlered among those without calves. The two dates that do not show significant differences lie at the beginning and end of the calving period. At the start of calving the number of cows with calves was too small to obtain a sufficient sample and at the end the number with antlers was too small.

The cows-without-calves category (line B, Fig. 8) actually includes three classes of cows: first, barren cows; second, pregnant cows and finally, cows that gave birth but lost their calves ("deprived cows"). Assuming that 53 per cent

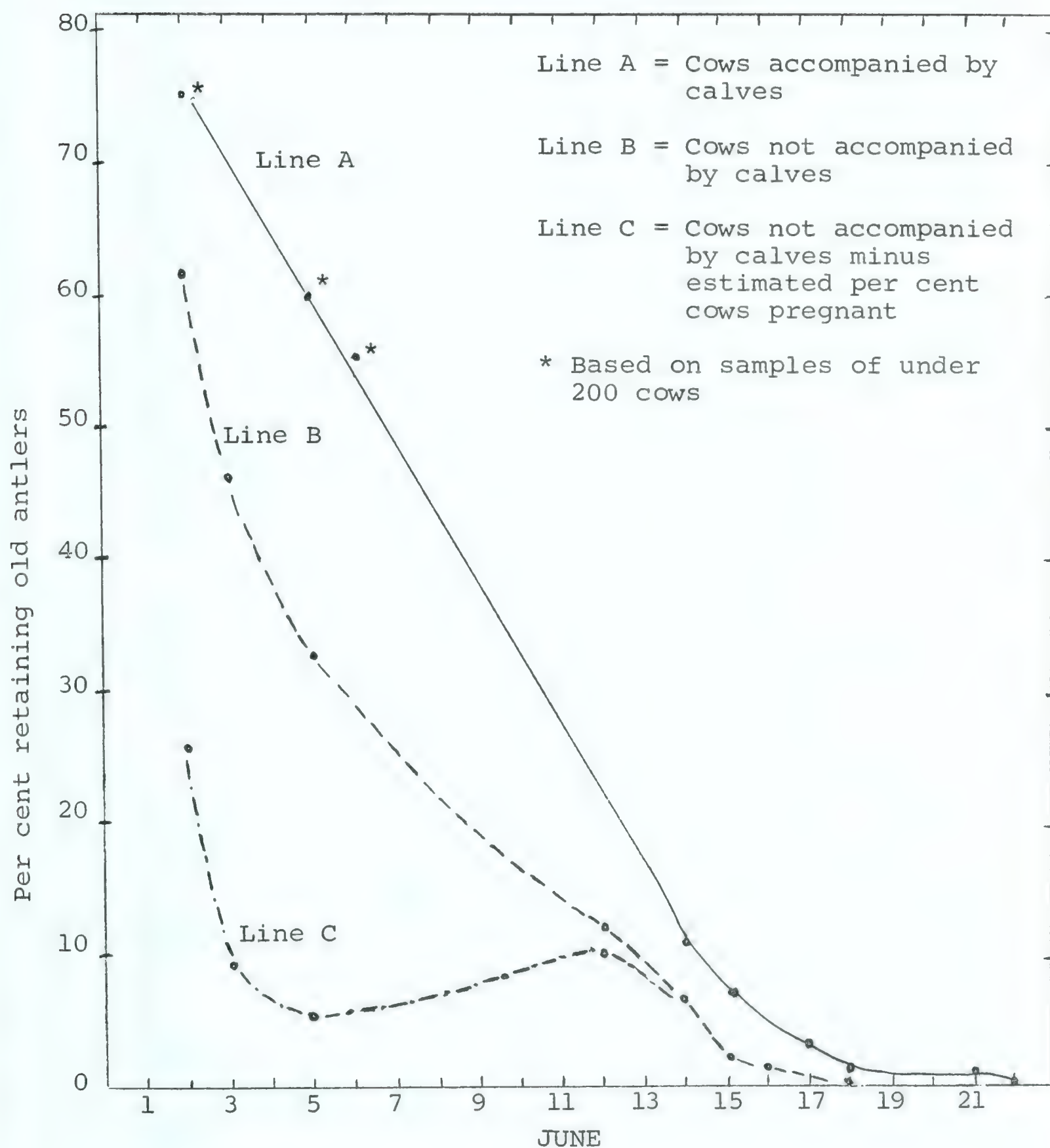


Fig. 8. Antler retention in caribou cows on calving grounds, June 1961.

Table 5. Proportion of antlered individuals among cows with calves compared with proportion antlered among cows without calves.

Date	Cows with calves			Cows without calves			χ^2*	P
	No. with antlers	No. without antlers	% with antlers	No. with antlers	No. without antlers	% with antlers		
1961								
June 2	6	2	75	142	91	61	<1.0	>.10
June 5	21	14	60	72	154	32	10.3	<.01
June 7	23	17	56	18	90	17	24.3	<.001
June 14	81	636	11	30	381	7	4.7	.05>P>.02
June 16	16	994	2	12	1683	1	4.7	.05>P>.02
June 18	5	537	1	1	635	0.2	3.5	.10>P>.05

* Test of significance of difference between proportions.

is an estimate of the proportion of cows pregnant at the start of the calving season and knowing the proportion of cows with calves on any given day during the calving season, it is possible to arrive at an estimate of the proportion of cows still pregnant on any day during the calving season. This proportion has been subtracted from the total proportion of antlered cows in the cows-without-calves category for each of the dates plotted in Fig. 8. The result of this calculation is an estimate of the proportion of cows with antlers among those that were either barren or had lost their calves. This estimated proportion is shown by line "C" in Fig. 8.

The high proportion (mean of 20 per cent) of antlered cows among those without calves but not pregnant in the June 2 and June 3 counts shows that not all barren cows have shed their antlers by the start of the calving season. These antlered cows without calves are clearly not all deprived individuals since for this to be the case then the calf mortality would have to exceed the number of calves alive on these dates. However, there appears to be a sharp increase in the rate of antler shedding among cows without calves in the first week of June. There was no reason to suspect that the ratio of calf mortalities to calf births varied appreciably throughout the calving season. The rise in line "C" during the latter half of the calving season is explainable by the increasing total number of deprived cows following the peak of calving and the end of antler shedding among barren cows before the calving peak.

The data do show that the majority of barren cows have lost their antlers by the beginning of calving. However, the proportion of cows with antlers before calving appears to underestimate slightly the proportion pregnant. This tendency towards underestimation was also shown in the work of Skoog (1959) where in each of 4 years the difference between the proportion "antlered" before calving and the proportion "with calves" after calving was too small to account for calf mortality.

On June 22, 1961, approximately one week after the end of calving, I observed 2,537 cows of which only five (0.2 per cent) were antlered. All five were accompanied by calves. Of an additional 1,600 cows observed from June 24 to July 9, none ~~were~~ ^{was} observed to have old antlers. These data indicate that all cows giving birth at the end of the calving season had shed their old antlers within one week after the season ended. Furthermore, an estimated 12 per cent of the total calf crop was born in the last 7 days of calving (June 8 to 15) and the proportion of cows-with-calves that still retained old antlers on the final two days of calving was 11 per cent.

My interpretation of these facts is that the cows retained their old antlers for an average of 7 days following parturition, at least among those cows giving birth in the late phase of calving. This figure is identical to that given by Popov (1935) for reindeer cows. Flerov (1960) quotes Semenov-Tyan-Shanskii as stating that the period between

parturition and antler shedding is 3 to 7 days among the wild reindeer of the Kola Peninsula. (See addendum, p. 209).

Composition of Calving Groups

One of the most universally observed traits in the migratory behavior of caribou and Palearctic reindeer is the segregation of the sexes which occurs before and during calving. According to Jacobi (1931) this phenomenon was first described by Pallas in 1811. The segregation may be so complete that by the actual calving time males make up only a fraction of 1 per cent of the animals over 2 years old in the central calving area (see Skoog, 1957; Kelsall, 1957). The development of this annual segregation may differ from area to area, however. Some observers have reported segregation on the winter range (see Banfield, 1954; Pruitt, 1960).

In northwest Alaska no large-scale segregation was observed on the winter range, certainly none at the southern boundary of the range, as Pruitt describes. Males did predominate in some upland areas on the north coast. Generally speaking though, the segregation developed gradually during the months preceding calving and was not completely evident until May. Of course, such a gradual process could also be explained by greater sensitivity on the part of females to changing snow conditions, as Pruitt suggests.

In the 1961 calving season only three (0.24 per cent) adult males, were observed in a sample of 1,264 individuals including calves. The few males observed on the

calving grounds are predominantly young individuals, 2 or 3 years old. Mixing of the sexes begins near the end of the calving season so that as the postcalving migration progresses there is a decreasing segregation of the sexes.

Since caribou groups show a high degree of openness (permeability) and are of a temporary nature, it was often difficult to precisely delimit such groups. Commonly one saw, let us say, 20 animals together, but also three or four others scattered at a distance of from a few yards up to a quarter of a mile. The decision as to whether or not to include such scattered individuals with the one group or treat them as separate groups could not be made without some subjectivity. Generally, however, units could be distinguished in which the movement and activity showed some coordination and often differed from that of other such units nearby. Even during relatively short periods of observation individuals could be observed to drop behind or move ahead of one such unit and be joined up by or join up with another unit. Thus a continual dynamic process could be observed.

In groups of several hundred or more individuals the synchronization of activities is far less evident. Such large groups, however, are isolated from one another by greater distances and appear more distinct. This makes delimitation easier.

Only observations made on the ground, when classes of individuals could be positively identified, are used in the following consideration of group composition and size.

The delimitation of groups was more difficult from aerial observation, in part because of disturbance of the caribou under observation.

To demonstrate changes in the size and composition of calving groups, the actual calving period was divided into three phases, of unequal length, representing the early, peak and late periods of calving. The exact lengths of these phases are given in Table 6. This table summarizes data on group sizes during these three phases of calving in 1961 and 1962 and from the precalving period (the week preceding the first observed birth) of 1962 and 1963.

Because of the wide variation in the size of groups, from 1 to 2,500 individuals, the mean size of the groups observed has little meaning by itself. In Table 6 the groups are placed in size categories that more clearly demonstrate the changes that occurred. There was some tendency for the smallest groups, one, two or three animals, to be missed while scanning the terrain and to pass by unnoticed during observations on larger groups thus some error undoubtedly occurs in the data presented. In view of this source of error, together with the problem of defining groups mentioned above, the data are presented here only as indicators of gross changes in calving groups.

By comparing the number of groups in the different size categories it may be seen that the increase in the mean size of groups late in the calving season was due to the formation of groups of over 100 animals in both 1961 and 1962.

Table 6. Size of caribou groups during early, peak and late phases of calving, 1961, 1962 and 1963.

Size of groups		Number of groups observed in each size category											
No. per group		Precalving			First 5-7 days of calving			Peak of calving (4 days)			Late calving 4-12 days after peak		
		1961	1962	1963	1961	1962	1963	1961	1962	1963	1961	1962	1963
1 - 4	--	5	5	12	23	15	8	13	--	7	7	--	
5 - 10	--	5	4	5	12	7	3	6	--	5	2	--	
11 - 50	--	11	9	3	5	13	8	4	--	6	4	--	
51 - 100	--	1	3	1	2	2	1	2	--	2	2	--	
101 - 500	--	1	0	1	1	1	2	0	--	8	4	--	
501 - 1000	--	0	0	0	0	0	0	0	--	6	1	--	
Over 1000	--	0	0	0	0	0	0	0	--	5	0	--	
Total all sizes	0	24	21	22	43	38	22	25	0	39	20	0	
Mean no. caribou per group	--	17	26	19	19	16	34	12	--	347	130	--	
Mean no. caribou per group with-calves	--	--	--	13	14	--	58	20	--	461	269	--	

In spite of this gross similarity between events in 1961 and 1962 other data for the two years were quite different in both the size and composition (Table 7) of groups. Aerial observations made in both years indicated that the sampling in 1961 was done within the main mass of the central calving segment, while in 1962 counts were made slightly towards the periphery. In addition, in 1962 the calving segment of the population was more scattered because of the unusual snow conditions, described elsewhere, that prevented some pregnant cows from reaching the calving area before parturition.

In spite of the progression of calving, which results in a continual increase in the total number of calves, the cow-to-calf ratio in the groups with calves is no lower in the late calving period than it is in the peak periods or in the early period in 1961 (Table 7). This relative stability of cow-to-calf ratios is understandable in the light of two other occurrences after the peak of calving is passed. First, there is a sharp rise in the proportion of groups in which calves are found. Second, there is an influx of young, non-breeding cows into the calving groups. The movement of these individuals from the periphery towards the main calving segment was observed in June, 1963 when I inadvertently camped outside of the calving area. At the same time there is an increased mingling of yearlings with cows and calves as the groups coalesce. This is evident in the striking increase in groups with both calves and yearlings in the late

Table 7. Changes in composition of groups on calving grounds, 1961, 1962 and 1963.

	Precalving		Early calving		Peak calving		Late calving	
	1962	1963	1961	1962	1961	1962	1961	1962
Total no. groups obs.	24	21	22	43	22	25	39	20
Groups with yearlings	19	16	9	21	13	16	37	11
	79	76	41	49	59	64	95	55
Groups with calves	--	--	9	11	9	10	31	11
	--	--	41	39	41	40	79	55
Groups with both calves and yearl.	--	--	2	5	2	4	29	6
	--	--	9	9	9	16	74	30
<u>In Groups with calves</u>								
Mean no. cows per group	--	--	4.7	14.3	6.7	38.6	11.0	306.0* 85.7**
Mean no. calves per group	--	--	2.6	2.0	1.5	12.8	8.5	123.0 49.0
No. cows per calf	--	--	1.8	7.2	4.5	3.0	2.5	1.7
<u>In Groups without calves</u>								
Mean no. cows per group	--	--	24.4	15.0	--	5.8	15.0*	3.1**

* $\bar{X}_1 = 306$, $s.d._1 = 159$; $\bar{X}_2 = 15$, $s.d._2 = 13.7$; $t = 4.3$, $df = 24$, $P < .01$

** $\bar{X}_1 = 85.7$, $s.d._1 = 161$; $\bar{X}_2 = 3.1$, $s.d._2 = 5.2$; $t = 4.44$, $df = 17$, $P < .01$

calving phase of both 1961 and 1962 (Table 7).

It is difficult to classify the groups of individuals observed on the calving grounds. Perhaps unavoidably, any such classification scheme tends to obscure the essentially dynamic process taking place. Pruitt (1960) describes three types of groups that he observed: "maternity bands", "false nursery bands", and "true nursery bands".

In the early part of the calving season there is some tendency for cows with neonate calves to join together, partly because they are similarly hindered in their movements by the presence of infants. The splitting off of such individuals from their previous groups will be described in detail in the section dealing with parturition and behavior after parturition. This splitting off probably accounts for the greater frequency of small groups (under 10 individuals) in the early calving compared with the precalving periods of both 1962 and 1963. After the peak of calving, however, the tendency to coalesce is greater among groups composed primarily of mothers than it is among other groups. This results in the number of cows-per-group in groups with calves being significantly larger ($P < .01$) on the average than the number of cows-per-group in groups without calves (Table 7).

The associations of cows with calves that start to form at about the peak in calving correspond to the groups which Pruitt calls "nursery bands". These groups include large numbers of calves of similar age (Fig. 4) as a result of the pronounced peak in calving. Thus the calf whose first

days are spent in such a group develops in a different social environment during these first days than the calf born early in the season (compare the mean number of calves per group for the different phases of calving in Table 7).

After the peak of calving nursery bands are continually coalescing to form larger and larger groups. This process is more pronounced at the center of the calving area. Towards the periphery, nursery bands retain a more distinct identity longer. By the end of the calving season groups of over 1,000 are common. These groups continue to coalesce in the postcalving period (Section 7).

Nursery bands and maternity bands are not only recognizable by their composition but also show some characteristic behavior patterns. The behavioral differences between such groups are discussed in Section 8. Pruitt considers the "false nursery band" to be a temporary aggregation of cows and newborn calves, an intermediate between the maternity bands and nursery bands. I was unable to distinguish any such aggregations.

In both 1960 and 1961 the proportion of yearlings to cows in the central calving area was approximately 40 per cent of the yearling to cow ratio in the postcalving movement (Table 2). Since not all cows are present in the calving area, but only approximately 90 per cent of them, the actual proportion of all yearlings that enters the central calving area is something less than 40 per cent. Aerial observations made during the calving season in the

peripheral calving areas and in areas that the precalving movements had passed through revealed groups composed primarily of yearlings, bulls and barren cows.

Not only do yearlings tend to remain on the periphery or outside of the calving area but those within the calving area tend to be found in groups in proportion to the number of barren cows, particularly around the start of the calving season. An analysis of 40 groups seen in the central calving area in late May shows a high correlation coefficient ($r = .87$) between the number of unantlered cows in each group and the number of yearlings. This compares with a lower correlation ($r = .69$) between the total number of cows in these same groups and the difference between the measures of correlation is significant ($P < .01$, see App. C, p. 218). Not only is there high correlation between the number of antlerless cows and the number of yearlings in each group, but also the number of yearlings in each group tends to approximate the number of antlerless cows in the same group. The importance of this correlation is based on the assumption that the majority of unantlered cows at the start of the calving season are barren.

Weight of Calves

The mean weight of 32 calves in their first day of life was 13 pounds (Lent, 1961). No significant difference ($P > .05$) was found between the birth weight of males and females nor was there any significant difference between the weights of calves born early in the calving season as compared with those born late.

Fig. 9 shows the weights of 29 calves from the Alaska study population collected during various months in 1961 and 1962 by O. Lønø. As may be noted from the graph the weights of calves increased rapidly until September and October but it appears that during the winter months calves did not increase in weight.

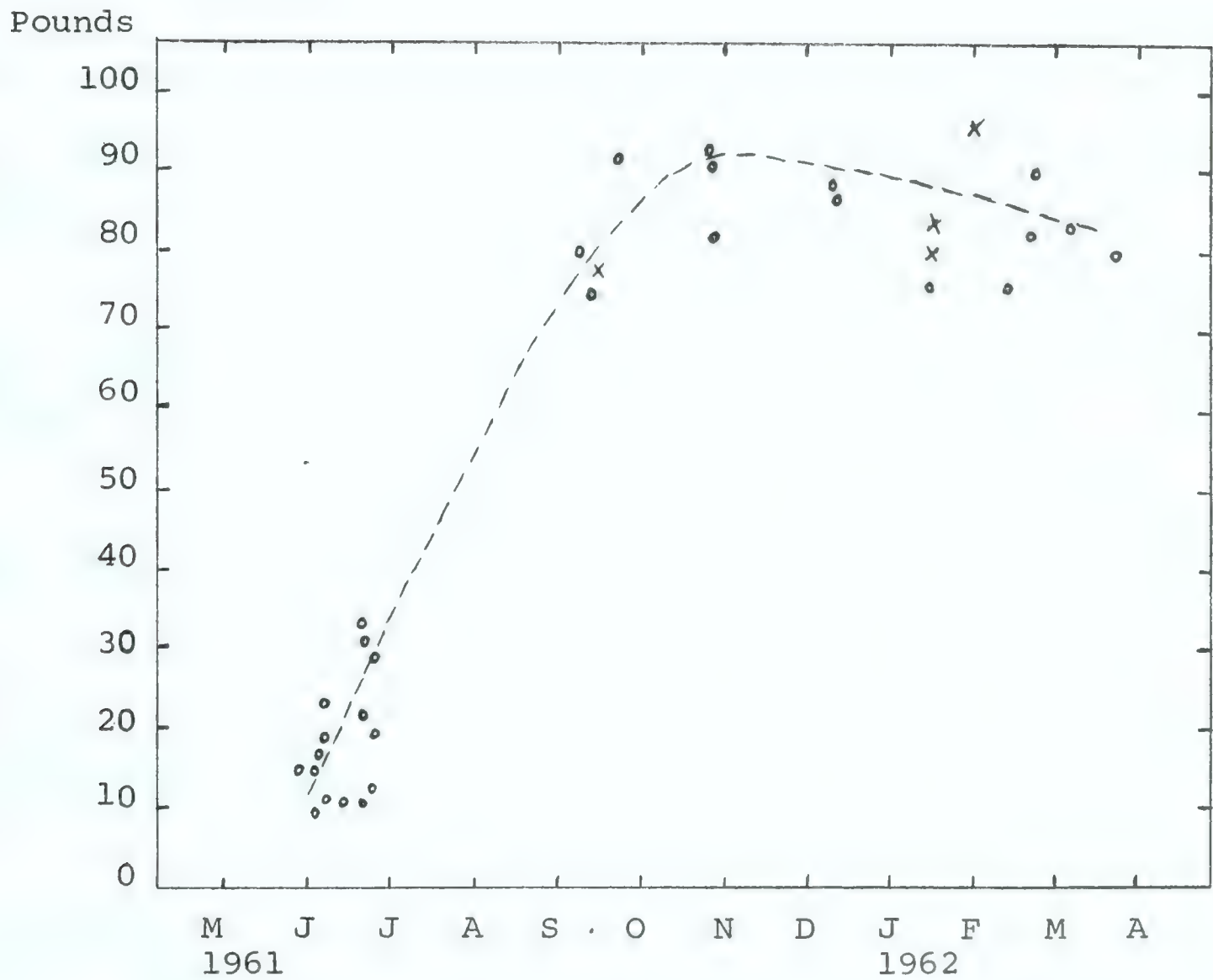


Fig. 9. Weights of caribou calves collected from May to March in northwestern Alaska.

○ male

× female

(only weights of males shown in May and June)

V. DISCUSSION

The Place of Calving in Relation to the Migratory Habit in the Genus Rangifer

Banfield (1954) emphasizes the variability of caribou movements on the Canadian barrens and concludes that the caribou must be considered nomadic, because its movements vary so much from year to year according to a variety of factors. Kalela (1961) also considers the caribou exceptional in comparison with other migrants in that it may completely change its winter or summer range from year to year.

Large scale shifts in range by caribou populations are described by Kelsall (1955) and discussed by Kalela (1961) and an example of this phenomenon is also cited in Skoog (1959:26). In this latter example, thousands of caribou left their normal range in Interior Alaska in autumn and continued north in the spring into northwest Alaska. Since the number of caribou in the original range of these individuals remained low for years afterward it is assumed that they never returned. The chances for permanent establishment of such emigrants are increased when the original population inhabiting the area they enter is at a low level, as was certainly the case in northwest Alaska.

Phenomena such as those mentioned above may be comparable to the "irruptions" and "vagrant migrations" observed in many migratory insect and avian species (see Wynne-Edwards, 1962). The degree of similarity cannot be ascertained until

we have a better understanding of the relationship between caribou populations and their environments. Indeed, many of the shifts in range that have been observed may be due to the effects of man on both the population levels and the habitats of caribou.

The caribou is confined to the surface of the land in its migratory movements and its locomotory powers are limited compared to those of volant migrants. Since the environment through which it must pass varies greatly from year to year, particularly regarding nival conditions, to which the caribou react with great sensitivity (Pruitt, 1959), it is not surprising that the caribou's routes of movement are more variable than that of migratory birds or sea mammals.

In the discussions of caribou and reindeer migrations mentioned above, little attention has been paid to the importance of calving grounds. Writers, such as Herre (1955) and Kalela (1961) who have emphasized the variability of the summer and winter ranges have neglected to consider the calving grounds. This neglect is partly explainable by the lack of information regarding calving areas and the short duration of the calving period.

Banfield (1954) states that there are no special geographic calving grounds in the Canadian barrens. He considers that the calves are born wherever the mothers happen to be during their spring migration, depending upon the conditions of the spring. Kelsall (1957) makes contradictory statements on the subject. At one place (p. 31) he states

that his continuing study bears out Banfield's conclusion that there are no specific calving grounds and the calves are dropped wherever the cows happen to be. However, on page 30 he states: "The cows at this time [right before calving] have the appearance of possessing a purpose or instinct to reach a specific area by a specific time."

Kelsall (1957), as well as other observers, has noted that the cows most advanced in pregnancy tend to arrive at the calving grounds first. I saw some indications of this tendency but it was not well defined because many groups of cows wintered close to the calving grounds and these groups arrived earlier than others, regardless of their stage of pregnancy. In 1961 particularly, many groups were observed to enter the calving area before the first births and continue moving in a circular pattern within the area until the calving season.

Unfortunately, there have not yet been any large scale tagging and recovery programs on caribou calving grounds. However, there is other evidence that the area of calving represents a comparatively fixed point in the movements of some caribou and reindeer populations.

I have already presented anthropological and historical evidence showing that the calving grounds and adjacent areas on the Utukok and upper Colville Rivers have remained as a relatively stable focal point for the population for at least a century, in spite of marked changes in the size and dispersal of the population. As the population declined the

length of the annual migration decreased by withdrawal from peripheral winter ranges.

Skoog (1959, 1961) shows that the calving grounds of the Interior Alaska "Nelchina Herd" also remained relatively fixed in the last decade in spite of changes in the winter ranges of this growing population. In 1956 the calving areas were shifted and dispersed somewhat, apparently due to unusual snow conditions in the normal calving area (Skoog, 1957). There are also indications that the calving areas and summer ranges of the "Steese" Herd in Alaska have remained more constant than the winter ranges (Skoog, 1956).

Fidelity to a specific calving area is suggested in some reports dealing with the introduction of reindeer into Alaska. For example, Jackson (1897) described how after an overland transfer of herds to newly established reindeer stations, cows sometimes showed tendencies to return towards their former station at calving time. Palmer (1926) also described how a group of transferred individuals returned to their original herd some 200 miles away, but he did not state at what time of year this occurred.

Sablina (1960) notes that when a reindeer herd was transferred from one area to another on the Kola Peninsula it was necessary to keep it enclosed to prevent it from returning to its old station. The herd was kept within an enclosure from April to November. Mr. Y. Espmark, University of Stockholm (pers. comm., 1963), also reports that female reindeer in Sweden are known to return to the same calving grounds from year to year.

The winter of 1961-62 was one of exceptionally heavy snowfall throughout the western end of the Brooks Range. In addition, the spring of 1962 was quite cool; the beginning of melting was delayed until the latter half of May. The unusually deep snow prevented many females from reaching the Utukok River calving area. Many calves were born on the south side of the Brooks Range where calving had not previously been reported. After this, however, almost all the cows that had not reached the calving area continued along the precalving routes as soon as their new calves were able to travel. Most of them continued onto the southern part of the calving grounds and then swung off on a post-calving movement similar to that observed in previous years.

This observation, as well as the others cited above, seems most easily explained by postulating a traditionally determined calving area.

In regard to the role of tradition in relation to the calving grounds, the location of yearlings during the precalving and calving periods is of interest. I have shown that 40 per cent or less of the yearling segment of the population enters the central calving area with the cows. Skoog (1957) has also made yearling counts on calving grounds in Interior Alaska showing a significantly lower proportion of yearlings in contrast to counts made both before and after calving.

Skoog's work (1956, 1957) also provides the only indications that female yearlings may be present on the

calving grounds in greater numbers than male. Skoog also found that the proportion of female yearlings on the calving grounds was significantly greater than 50 per cent in both years in which samples were taken. Although the actual sex ratio in the yearling age class has not been determined from counts outside of the calving period, this suggests that female yearlings are more likely to enter the calving area. Kelsall (1960) does present some data indicating higher mortality among male calves in the Canadian Arctic.

In many ungulates male yearlings are separated from the mother earlier than female yearlings. Eygenraam (1963) believes this difference in red deer (Cervus elaphus), is due to the sexual play of male yearlings which tends to generate antagonism on the part of the mother. Female yearlings of this species may resume nursing after the mother has given birth to another fawn. Dasmann and Taber (1956) indicate that in the Columbian black-tailed deer (Odocoileus hemionus columbianus) the male yearling is more likely than the female to be permanently separated from the mother at her subsequent calving time. Similarly, in the wildebeest (Gorgon taurinus) male yearlings form bands but the female yearlings usually remain with the mother after the birth of the new calf (Talbot and Talbot, 1963). R. C. Bigalke, Alexander McGregor Museum, Kimberley, Union S. Africa, (pers. comm., Aug., 1963) suggests that a similar earlier separation of male yearlings into bands occurs in many species of African antelope.

Assuming that it is primarily the female yearlings that return with the caribou cows to the calving grounds, then both the ortstreue ("homing tendency") at calving time and the precalving separation of the sexes in older age-classes would be reinforced.

Phenology of Calving

In Table 4 I have compared the summaries of weather conditions during two calving seasons and some incomplete information on a third calving season in northwest Alaska with the summaries given by Kelsall (1960) for 3 calving seasons in the Canadian Arctic calving grounds near Beverley Lake. The Alaskan summaries are based on data for the last week of May and the first 3 weeks of June. The Canadian data are for the month of June. In both cases the periods covered by the data are those in which essentially all the calves are born plus a few days afterward.

The weather in the Utukok River calving area in 1961 and 1962, as well as in 1960 and 1963 when less detailed weather records were kept, was considerably milder than that recorded in Canada in 1957 and 1958 but similar to the weather in 1948.

Of particular interest is a comparison of the daily wind chill measurements. Kelsall (1957, 1960) described how severe weather conditions may result in high calf mortality. More specifically, he suggested that high calf mortality occurs during days when the wind chill factor reaches 1,000 or

more. As is shown in Table 4 this is an infrequent event in Alaska, in comparison with the Canadian area. In no day did the wind chill exceed 1,000 in the three calving seasons (1961-1963) in Alaska. Wind chills in excess of 1,000 were recorded on 14 days in 3 seasons (1948, 1957, 1958) in Canada.

The number of dead calves found by us in Alaska was far smaller than that reported by Canadian workers in spite of the daily activity of 5 or 6 men in the calf-tagging crews in both 1960 and 1961 (see Lent, 1961). This suggests that calf mortality was lower in these years than that reported in Canada.

The vegetation available to the cows during calving also differs greatly between the northwest Alaska calving area and the Canadian Arctic area. In Alaska the budding of Eriophorum and the melting of the snow cover occurs by the start of calving. In Canada new growth of Eriophorum is not apparent until after June 15. During calving the food consists of lichens and withered vegetation on the snow-free ridges. Such a contrast in available food could result in important differences in calf survival and development between the two regions.

Soviet workers have all emphasized the important influence of the quality of forage available to cows during late pregnancy and during the calving season on the survival and development of reindeer calves (Ivanova-Drury, 1938; Ponomarev, 1938; Gulchak, 1954). Thus it would seem that more attention might be paid to the role of spring forage

and the condition of cows at calving time in attempts to understand the factors influencing annual recruitment in caribou populations.

There is little doubt that the level of initial calf survival among the Canadian Arctic caribou would be higher if the peak of calving occurred in the last half of June, but there are factors that might operate against a later calving period. Late-born calves might be more affected by the attacks of mosquitoes and other insects; Popov (1935) suggests this and Krebs and Cowan (1962) describe how the growth of late-born calves kept in a pen stopped after the start of the mosquito season. Russian workers have also emphasized the necessity for calves to obtain a minimum weight in order to survive the winter (Ivanova-Drury, 1938; Ponomarev, 1938).

Ponomarev shows that in domestic reindeer the calves born near the end of the calving season are lighter in weight on the average than those born earlier and are predominantly the offspring of the younger cows (Table 8). Clegg (1959) states that there is little clear-cut evidence to prove a relationship between age of the mother and length of pregnancy in any domestic animal. He also states that prolonged pregnancy results in larger-than-average calves with a slow post-term growth, at least in domestic cattle. If these statements are applicable to reindeer also, it would seem that later births are more likely due to a delay in fertilization rather than to a prolonged gestation. According to the data of Ponomarev (1938) the initial growth rate of

Table 8. Average birth weights and growth rates of reindeer calves according to time of birth during the calving season. (Translated from Tables 12 and 17, Ponomarev, 1938).

Time of birth	N	Mean birth weight (Kg)	Total growth (as per cent of original weight).			
			<u>First month</u>	<u>Second month</u>	<u>Third month</u>	<u>Fourth month</u>
Early in season	30	6.48	224	432	631	784
Peak of season	30	6.34	267	454	652	786
Late in season	26	5.79	297	513	789	---
Mean	86	6.20	261	462	672	---

late-born reindeer calves is actually greater than that of the calves born earlier (Table 8).

The fact that the start of the calving season is much more abrupt than the end also suggests that unusually timed births are not primarily a result of variability in the gestation period. Schmitt (1936) claimed that females fecundated near the end of the rutting period had an average period of gestation 6 to 7 days shorter than those fecundated at the start of the rut. If this were so then the peak period of calving would be accentuated in comparison to the peak of rutting activity. Gorbunov (1939), however, states that his data do not support Schmitt's conclusion.

The phenology of calving has been examined closely in several Rangifer populations. In Table 9 I have summarized the findings of various studies dealing with both caribou and Palearctic reindeer populations.

The data upon which Table 9 is based were collected in several different fashions and the results are presented in the literature with widely varying preciseness. For these reasons the original sources should be consulted for more detailed comparisons of the populations. In many cases the original sources date the start, peak and end of calving as occurring within a 3 or 4 day period. For these cases I have presented only the median date. In addition, workers have used different criteria for determining the dates of calving. The "peak" date may be considered the date by which 50 per cent of the calves are born or it may be the date on which

Table 9
Overleaf

Table 9 Phenology of calving and rutting in populations
of Rangifer tarandus

Location and nature of population	Calving lat. (deg.)	Calving Start	Calving dates ¹ Peak	End	Dura- tion (days)	Approx. peak rutting ²	Lat. of rutting ³ (deg.)	Approx.No. hours day- light at rut peak ⁴	Source of Calving data
Gaspe Peninsula, wild, non-migr.	47-48	May 12	May 22	June 4	24	Oct. 7	47-48	11:20	Bergerud, 1961
Newfoundland, wild, short migration. 1958 1959 1960	48-50	May 23 May 21 May 23	May 28 May 29 May 29	June 2 June 3 June 4	11 13 13	Oct. 13	48-50	10:55	Bergerud, 1961
Kamchatka, U.S.S.R.	55-60		late June ⁵		?	mid Nov.		8:05	Flerov, 1960
Northwest Terr., wild, migratory. 1959 1960 1962		June 10 June 7 June 2	June 14 June 11 June 12	June 16 June 12 June 16	7 ⁶ 6 ⁶ 14	Oct. 28 Oct. 25 Oct. 26	60-62	9:05 9:20 9:10	McEwen, 1959 McEwen, 1960 McEwen, 1963
"Nelchina" Interior Alaska, wild, migr.	62-63	May 22	May 26	June 4	13	Oct. 9	62-63	10:35	Skoog, 1957
"Steese" Interior Alaska, wild, migr.	65-66	May 18	May 22	June 3	15	Oct. 4	64	10:55	Skoog, 1957
Golovin Bay, Alaska. Introduced from Chukotsk Peninsula, Domestic	64	Apr. 13	May 1	May 14	30	Sept. 16		12:50	Jackson, 1897
Northern Urals, U.S.S.R. Domestic	65	May 1	May 22	early June	one mo.	Oct. 4		10:55	Ponomarev, 1938

Chukotsk Peninsula, U.S.S.R.	65-66	--	--	--	--	Sept. 21	65-66	12:25	Vinogradov, 1936
MacKenzie Delta (as for Golovin Bay, above)	69	Apr. 20	Apr. 28	May 5	15	Sept. 13		13:30	Krebs & Cowan, 1962
Yamal District, U.S.S.R., Domestic	67-68	--	--	--	--	Oct. 17	67-68	9:30	Vinogradov, 1936
Murmansk, U.S.S.R. Domestic	68-69	May 1	May 1	June 3	11	Oct. 1		11:20	Flerov, 1960
				June 12	15	Oct. 7		10:45	Vinogradov, 1936
				June 12	12	Oct. 20		8:30	Lent, 1964
Eastern Alaskan Arctic, wild, migr.	69-70	May 30	May 30	June 14	14	Oct. 14		9:30	Skoog, 1962
Western Alaskan Arctic, wild, migr.	69-70	May 23	May 26	June 3	11	Oct. 9	68-69	10:15	
	1960	May 28	June 5	June 12	15	Oct. 19		8:30	
	1961	May 30	--	June 12	12	Oct. 20		8:30	
	1962								
South Georgia (Falkland Islands), wild, non-migr.	54 S.	November	November	--	--	mid March		12:35	Bonner, 1958

¹ See discussion in text.

² Calculated on basis of mean gestation period of 227 days, (Schmitt, 1936) and calving data.

³ If not given, it is assumed to be approximately the same as the calving latitude.

⁴ Smithsonian Institution, Meteorological Tables.

⁵ Based on time of rutting; Flerov (1960) does not cite original source of this information.

⁶ As calculated by Bergerud (1961).

the most calves are born. Most workers have used the latter, but many do not make it clear which is meant. The two events may be separated by a few days.

The "start" and "end" dates calculated for several populations by Bergerud (1961) (shown in Table 9) delimit the period in which 90 per cent of the calves are born. For comparison, I have adjusted the northwest Alaska calving dates, as they were shown in Table 3, to conform with his criteria.

I have already shown (Fig. 9) that caribou calves in the study population did not appear to show any increase in weight during the winter of 1961-1962. There is some evidence that reindeer calves also commonly show little or no growth during the winter months. Ponomarev (1938), in his discussion of selective breeding programs, divides calves into classes according to their desirability for breeding purposes, based in part on their weights. The weights that he gives for each class at the age of 13 months are exactly the same as those given for the classes at 8 months, before the start of winter. The data of Gulchak (given in Krebs and Cowan, 1962) also show the great similarity between calf weights in December and yearling weights in June. Ivanova-Drury (1938) states that September is the month of greatest absolute growth for the reindeer calf, in October rate of gain drops sharply. According to Alaruikka (1959), modern Soviet reindeer herders cull many 6-month-old calves for meat. An average yield of 30 Kg may be obtained at this age but this yield increases to only 40 Kg per yearling a full year later.

In those cases where the calves show a temporary cessation of growth in weight it seems quite likely that the winter conditions for calf survival must be marginal. Ponomarev's work demonstrates that the probability of survival through the winter of a reindeer calf is correlated positively with its weight at birth. Furthermore, the mean weight of reindeer calves at birth is correlated positively with the weight and age of the mother.

In view of the importance of high initial weight and growth rate for calf survival it is not surprising that there are no proven cases of twinning in barren-ground caribou. Twins do occur rarely among domestic reindeer (Jackson, 1896, 1897) but according to these reports the cow will not accept or care for the second calf. Observations of two calves following the same cow (Moisan, 1959; McEwen, 1963) do not prove the occurrence of twins since calves will frequently associate temporarily with a strange cow, especially when groups have been disturbed.

The approximate number of hours and minutes of daylight at the estimated peak of rutting for each population is also included in Table 9. The wide variability that is evident does not in any way preclude the hypothesis that the length of the daylight period is the external factor by which the reproductive cycle within a population is synchronized. The reindeer introduced from Norway to South Georgia Island in the southern hemisphere reversed their breeding periods to correspond with the reversed seasons in a manner similar to

other ungulates introduced to that hemisphere (Bonner, 1958).

There is some indication of a tendency for calving to occur later at higher latitudes but there is no clear trend for the period of calving to be more restricted at higher latitudes. Such a trend might be evident if more accurate information were available. In particular, comparative data from populations on the Arctic Islands of Canada and from the Alaska Peninsula would add to the knowledge of tundra-dwelling caribou at two extremes of latitude within the range of the species. Jacobi (1931) believed the rut occurred earlier in more northern populations but there is no evidence to support this contention.

Sdobnikov (1958) reports slight differences in the calving times of wild reindeer that migrate inland on the Taimyr Peninsula compared with those that remain and calve on the Arctic Coast (about 2 degrees farther North). Domestic reindeer in the same general area calve a full month earlier. However, Sdobnikov also cites the work of Semenov-Tyan-Shanskii who found that wild and domestic reindeer on the Kola Peninsula had identical calving seasons.

In all wild, tundra-dwelling populations the period in which 90 per cent of the births occur is 2 weeks or less. Bergerud (1961) contrasts the less restricted breeding season of the Gaspé Peninsula caribou with these tundra-dwelling herds. Domestic reindeer also show a less pronounced peak in calving. Ponomarev (1938) reports 80 per cent of calving in a 15 day period in a domestic reindeer herd of the Ural

Mountains. In contrast, McEwen (1963), working with barren-ground caribou, recorded 80 per cent of births in a 5 day period in 1959 and 87 per cent in 5 days in 1960. These caribou, in the Canadian Arctic show the most restricted calving season and also make the most extensive migration of any Rangifer population. I have already shown that these caribou are apparently subject to more severe weather conditions during calving than are the northwest Alaska caribou, in spite of their somewhat later calving period.

It would seem that the time of birth must represent a compromise. If the calves are born too soon they are more likely to encounter unfavorable weather conditions leading to high mortality. Calves born too late are more likely to succumb to conditions marginal for survival in the winter following their birth.

It must also be recognized, however, that some workers (Skoog, 1959; Kelsall, 1960) have reported a larger calf mortality in the summer months than in the winter months of certain years. Little is known about factors that might influence the level of calf mortality during the summer months. There are factors related to the migratory behavior of barren-ground caribou that might also result in greater mortality among late-born calves. These are discussed in Section 8, after the behavior patterns involved have been described.

VI. BEHAVIOR DURING THE CALVING PERIOD

Behavior Associated with Parturition

An attempt was made to determine whether any particular type of terrain was preferred by cows as a site for parturition.

Notes taken on the location of 16 cows seen during labor or immediately after giving birth are summarized in Table 10. It is not surprising that 11 out of the 16 cows gave birth in the Eriophorum tussock community. This is the predominant community of the calving grounds both in terms of area and in terms of importance for food. Thus no strong site selection was indicated, although very wet sites within this community were avoided. There is a tendency for some individuals to move up-slope before parturition. This tendency was seen most clearly in an older cow on May 29, 1963.

Two cows observed on June 3, 1962 (Table 10) gave birth in the midst of a snowstorm on a surface of fresh and old snow. The wind at the time was 15 mph; the temperature, 32 F; and heavy, wet snow was falling. These cows were not situated in a sheltered location although shelter was available within one-half mile.

There was little tendency for cows to seek seclusion at the time of birth. Of the 17 parturitions noted in Table 10, about half occurred within groups or in close proximity to other individuals. Of those cows observed to give birth alone, only two were seen to deliberately move away from the

Table 10. Time and site of 17 parturitions.

Date	Approx. time	Terrain, Vegetation*	Site in relation to other caribou
<u>1960</u>			
May 28	--	<u>E.</u> tuss.	In group of 20 cows and yearlings.
" "	evening	Wet meadow	Alone, but others scattered within 1/4 mile.
<u>1961</u>			
June 2	0930	<u>E.</u> tuss., along river	On outskirts of loosely scattered band of 200-250 feeding and resting cows.
" "	1600	Depression with low willows	Another cow and calf few yards away.
" "	2130	<u>E.</u> tuss.	Pregnant cow 5 ft. away, another cow with calf and a yearling few yards away.
" "	1330-1400	--	Alone.
June 4	1300	<u>D.</u> mat, ridgetop	Alone, but on pathway of migrating groups.
" "	1400	Wet meadow	Alone.
June 5	1100	<u>E.</u> tuss., side of ridge	125 yards from nearest others.
<u>1962</u>			
June 1	1900	<u>E.</u> tuss., hillside	In group of 50 (stillbirth).
June 2	1230	<u>D.</u> mat ridgetop	Alone.
June 3	1330-1400	<u>E.</u> tuss., slope	2 births, cows together, none others nearby.
June 12	1800	<u>E.</u> tuss.	In midst of large group (stillbirth).
June 13	1200	<u>E.</u> tuss.	100 yards from group of 200+, mostly cows with calves.
" "	1500	<u>E.</u> tuss.	In midst of above group.
<u>1963</u>			
May 29	1900	<u>E.</u> tuss., hillside	Alone, traveled 1/2 mile from group before giving birth.

* E. tuss. = Eriophorum tussock vegetation type, drier than wet-meadows, usually on gentle slopes.

D. mat = Dryas mat vegetation type, xeric, predominantly Dryas octopetala. (See Johnson and Viereck (1962) and Spetzman (1959) for further description of vegetation types).

group. More often the cow stops to commence labor and is left behind by the moving group. If the group is resting when a cow is in labor, the birth may occur in the midst of the other individuals. This was the case in each of the three births observed on June 4, 1961, for example.

Another observation will illustrate how a cow may be left alone at parturition time without actively seeking seclusion. On the morning of May 25, 1963, the first two calves of that year were observed. One calf, about 3 hours old, and its mother were located half a mile from a group of 50 cows and yearlings. Another pair, this calf 4 to 6 hours old, was located a quarter mile from the same group. Both pairs were located along the route traveled by the group earlier in the morning. This was shown by the tracks in the snow, as well as by the general direction of travel of all groups moving through. The older calf and its mother were moving slowly towards the group to rejoin it and thus were closer to the group at the time of my observation. The younger calf was still at the spot where its mother had dropped out of the moving group.

In contrast, a cow observed May 29, 1963, left the group it was traveling with, and moved in the opposite direction and up-slope for almost one-half mile. This cow remained extremely nervous and alert until giving birth. It is possible that the cow had been frightened in some way while still in the group it had been traveling with.

The sensitivity of cows to any unusual stimuli reaches a peak just before they give birth. This sensitivity

was clearly seen in attempts to stalk cows. By far the most difficult to approach were those about to give birth or in the early stages of labor. Thus some observations of cows leaving groups before giving birth may perhaps be explained by unknowing disturbance of the cow.

The time of birth was noted for 16 of the parturitions listed in Table 10. Seven of the births occurred during the mid-day hours, but this number is not significantly higher ($P > .10$) than the number observed in the late afternoon hours, when an approximately equal amount of time was spent in observation. The small number of births in the night and morning hours are not of any significance because of the relatively few observations made in these hours and the difficulties with heat-wave distortion.

In Table 11 I have summarized my two most complete observations of parturition and post-partum behavior along with four previously published descriptions of this behavior in caribou.

As do most other ungulates, the caribou cow commences licking and cleaning the calf within a few minutes after its birth (App. A, No. 2). Although close observations were difficult to obtain and the infant was always somewhat hidden, even on the most barren terrain, it appears that the cows lick first the entire body of the calf and later concentrate more on the face, the posterior portion of the back and the anal region.

During the first hours of the calf's life there is always very frequent contact between the mother and the neonate.

Table 11. Summary of data on parturition and post-partum activity from five observers.

Observer	Lent		Pruitt
	<u>Observation "A"</u>	<u>Observation "B"</u>	<u>(5 observations)</u>
Duration of Labor (min.)	25	---	15-30
Position of Cow at moment of birth	Standing (in motion)	Standing	lying
Time after birth (min.)			
0	} Cow licks calf, feeds.	} Cow licking.	} Cow feeding and licking.
10			
20			
— Placenta passed.		— Placenta passes.	
30	} Calf attempts to rise.	} Licking, "gumming" at anal region of calf.	
40			
50			
60	— Calf standing.	— Calf standing, cow licks and knocks it down.	
		— First successful nursing.	
70		— When approached, cow fled, calf did not try to follow.	
80			
90	— Calf walking few steps.		Both cow and calf rest for 15 min.-1 hr.
120	— No suckling as yet, cow tries to follow others,		
125-180	— calf follows slowly.		
180-240			

Table 11 continued:

Observer	Kelsall (1957)	(Wilks' obs.)	Kelsall (1960)	(de Vos' obs.)
Duration of Labor	30	---	approx. 1 hr.	
Position of Cow	lying	lying	---	
Time after birth (min.)				
0	"calf standing within few minutes.	}	}	Licking. Placenta passed.
10				
20				
		}	}	Calf tries to rise. Calf walks few steps.
30	—Calf walking unsteadily.			
40				
50				
60				
70		}	}	Licking.
80				
90	—Cow and calf traveling several miles after disturbed.			
120	—Calf had suckled twice.			
125-180		}	}	140: walks for 2 min. 180: tries to nurse. 220: cow and calf leave.
180-240				

These contacts are of several types. Nursing and attempts to nurse occur with the greatest frequency during these first hours (see "Nursing" below), although the first successful suckling may be delayed until the second hour after birth, or later (Table 11). In addition, the cow is continually interrupting its feeding to lick the calf, particularly in the anal region. It often does so even when the calf is resting. Besides this actual licking the cow is often observed to approach the calf and extend its muzzle to it, many times making contact with the calf's muzzle or head region, sometimes on the body or the anal region. Often the cow will stop a few inches short of actual contact. Darling (1937) describes similar behavior by red deer hinds. A great similarity exists between these actions and those frequently observed when a cow and calf are reunited after a period of separation.

Observations of three neonates and their mothers for a total of 7 hours indicate a cow-calf contact of one of the types described above occurs approximately every 3 minutes, excluding time when both members of the pair were resting. The greatest frequency of contacts occurs when a cow is attempting to move with or to a group before her calf is able to travel steadily. Under such conditions two or three contacts a minute can occur.

In all cases where long periods of observations were obtained with undisturbed pairs, the cow attempted to travel within 4 hours after giving birth and elicited following in calves that had not yet fully attained the motor ability to keep pace.

Abnormal Births

In the course of my study several cases of abnormal births were noted.

1) A dead calf was found with the umbilical cord wound around its neck.

2) On two occasions a cow and calf were found dead together. In both cases parturition had taken place but the two were still joined by the umbilical cord. No injuries or other abnormalities could be found externally.

3) On June 13, 1962 an apparent stillbirth was watched for a period of over 2 hours. The cow remained in approximately the same spot, feeding, for most of the first hour. By the end of this hour more than three-quarters of the fetus could be seen protruding from the vagina. When last seen, after 2 hours, the cow was traveling rapidly in a large group. By this time she was giving no further reactions to the hanging fetus, which was by then almost entirely expelled. Earlier, she occasionally swung her head back towards it. The amniotic sac had ruptured during the first half-hour and by the end of the observation the fetus appeared completely dry.

4) In 1962 and 1963 several other cows were observed whose calves had apparently either been stillborn or died soon after birth. These cows were recognized by their behavior, by the presence of blood and matter in the area of the vulva together with the absence of a calf accompanying them, or by the presence of a dead calf. Since the presence

of brucellosis has been demonstrated in the caribou of north-western Alaska (Skoog, pers. comm., 1963 and 1964, and unpublished data) it seems likely that at least some of these stillbirths were in cows infected with that disease. Some cows were observed to retain placental material, often hanging to the ground, for several hours after delivery. These cows were traveling in groups either with or without calves. There also appeared to be an unusually large amount of dried blood in the area around the vulva and on the hind legs of these cows.

In two cases where parturition was not observed, cows with dead calves were seen right after giving birth. The cows made no attempt to lick or remain with the calf but moved off when the groups they were in moved. One of them, however, was observed to grunt occasionally and once moved away from the group towards the site of parturition. She returned to the same group in a few minutes.

5) Additional abnormalities were noted in a cow and calf collected on June 22, 1961. The cow had an infected uterus, the right horn of which was fused to the end of the caecum. The calf showed heavy infection of the umbilical region and an umbilical hernia from which a section of the small intestine protruded.

Nursing

The interval between the birth and the first nursing attempts as well as the occurrence of nursing as one of the types of frequent contacts between the cow and her neonate

calf have already been noted. Here, data on the position, frequency and duration of nursing will be considered, as well as other aspects of nursing behavior.

Data were collected on over 200 nursing events, including unsuccessful attempts to suckle. A single successful nursing event is defined here as the period from the moment the calf started suckling until it moved its head from the nursing position. Thus, if a calf momentarily removed its lips from the teat and then resumed suckling a separate event was not recorded. For unsuccessful attempts, a bout of attempts was recorded as a single event so long as no other behavior pattern (such as grazing, running, or scratching) was interposed.

Two basic nursing positions were of importance: nursing from the side, occurring 79 times, and nursing from between the hind legs, occurring 46 times. In 70 of the side-position events the calf was positioned at an acute angle to the cow with its rear towards the mother's head. With the calf in this position, the cow is able to lick the anal region of her calf and cows were observed to do so in 28 out of these 70 events.

The position of the calf while suckling was recorded for 130 successful nursing events. The frequency of the different nursing positions and of successful attempts from each position is shown in Table 12. The relationship between the suckling position and the duration of each suckling event is shown in Table 14.

Table 12. Frequency of success of nursing attempts from different positions.

Nursing Position	No. of attempts	No. successful	% successful	% of total suc. att.
<u>From the side</u>				
Calf's rear to the mother's head	--	70	--	54.0
Body axes at right angles	--	7	--	5.0
Calf's rear at mother's rear	--	<u>2</u>	--	<u>1.5</u>
Total from side	104	79	76*	60.5
<u>From between hind legs</u>	81	46	57*	36.0
<u>Other positions</u>				
Calf standing under mother's body	3	3	100	2.0
Nursing while mother lying down	5	2	40	1.5
Searching at mother's forelegs	6	0	00	00
<u>Total all positions</u>	199	130	65	100

* Comparison of proportions successful in 2 x 2 contingency Table shows $\chi^2 = 7.6$, $P < .01$.

On most occasions the age of a calf under observation was either known or could be estimated according to the criteria discussed earlier. Calves were divided into four age-classes: under 4 hours, 4 to 24 hours, 1 to 7 days, and 8 to 21 days. The proportion of successful nursing events and the frequencies with which the different nursing positions were used by each of these age classes are shown in Table 13.

Timing of the duration of suckling on 143 occasions yielded a mean suckling time of 32 seconds. This figure agrees with the observations of de Vos (1960). The differences in the mean duration of suckling events between the age classes were very slight (Table 13) and not significant ($P > .10$).

In 23 timed events in which the cow licked her calf the average duration of suckling was 64.8 seconds, compared with a mean of 27 seconds for 43 events in which the calf nursed from the side but was not licked. The difference is significant ($P < .01$, Table 15).

Of the attempts to nurse between the hind legs, only 57 per cent were successful compared with 76 per cent success rate in attempts to nurse from the side. The higher success rate in side attempts is statistically significant ($P < .01$, Table 12).

Attempts to nurse between the hind legs occurred most frequently when the mother was feeding and moving slowly (App. A, No. 5; Fig. 4). Frequently a calf would attempt to make contact while the mother was actually in motion. By

Table 13. Frequency of nursing positions and nursing success rate of different calf age-classes.

Position	Age-class				
<u>From Side</u>	<u>Under 4 hours</u>	<u>4 to 24 hours</u>	<u>1 to 7 days</u>	<u>8 to 21 days</u>	<u>Total, all ages</u>
Total attempts	25	25	32	11	93
Successful attempts	14	23	26	10	73
Per cent successful	56	92	81	91	78
<u>From Rear</u>					
Total attempts	19	22	45	10	96
Successful attempts	9	7	34	5	55
Per cent successful	47	32	76	50	57
<u>Other positions and unspecified</u>					
Total attempts	15	26	20	14	75
Successful attempts	4	13	10	7	34
Per cent successful	27	50	50	50	45
<u>All positions</u>					
Total attempts	59	73	97	35	264
Successful attempts	27*	43	70*	22	162
Per cent successful	46	59	72	63	61
Ratio - attempts to nurse from side: attempts to nurse from rear (=1)	1.3	1.1	0.71	1.1	0.97
*Test of significant diff., $\chi^2=10.9, P<.01$					
<u>Mean duration of suc- cessful attempts (sec)</u>					
	31.4	31.8	31.9	32.8	

Table 14. Duration of successful nursing events from side and from rear.

	Side	Rear
Mean (sec)	40.0	13.9
s.d. (sec)	43.0	12.1
df	72	45
t = 4.32 P<.01		

Table 15. Comparison of duration of side-nursing events with and without licking by the cow.

	With licking	Without licking
Mean (sec)	64.8	27.0
s.d.	53.4	20.3
df	22	42
t = 4.2 P<.01		

approaching from the rear the calf avoids being struck by the hind legs as often occurs in side-nursing. In some instances a calf was able to suckle by following along with its mouth on a teat while the mother was moving slowly. No calf ever attempted to block the forward movement of its mother before suckling, as has been observed in bovids (see Schloeth, 1958; Marjoribanks Egerton, 1962). These bovids, however, do not attempt nursing from the rear as frequently as caribou and rarely do so unless they are frustrated in a side-nursing attempt. Thus it appears that one nursing behavior pattern (blocking the mother) found in bovids is lacking in the caribou but another (nursing from between the hind legs) is more highly developed. Schloeth does describe one calf of the Camargue cattle (Bos taurus camarguensis) that "specialized" in nursing from the rear, doing this even when the mother was moving.

There are indications that among caribou, also, some individuals might use one position of nursing predominantly. One calf made 17 out of 20 observed nursing attempts from the rear of the mother.

The mean duration of suckling events from the rear position is significantly shorter than that of side-nursings ($P < .01$, see Table 14). Thus in spite of an approximately equal number of attempts to nurse from each of the two basic positions the "side" position is of greater importance to calves of all age-classes because of the higher success rate and longer mean duration.

The data on the proportion of attempts to nurse that were successful in each of the age-classes are of interest, although the sample sizes are small. During the first hours the success rate of the neonates is low due in part to the lack of motor development (often resulting in loss of balance before the teat can be grasped, for example) and in part due to an initial response, particularly by younger cows, to avoid the nursing attempts of their infants. If attempts to nurse at the forelegs are included, the rate of success in nursing attempts by this youngest age class is 46 per cent. Of the six observations of calves searching at the forelegs, five were of calves under 3 hours old, the sixth of a calf 5 to 6 hours old. Only one calf was observed in a second bout of foreleg searching, but it is probable that the 5-to-6-hour calf had also already made its initial nursing and was again searching around the forelegs.

The success rate during the first 4 hours is significantly lower than the rate after the first day ($P < .01$). The increased occurrence of failures after the first week is not significant ($.10 > P > .05$). Regarding the frequency of attempts to use the side-nursing position versus the rear-nursing position by the different age-classes, none of the differences are significant.

It was difficult to obtain quantitative data on the frequency of nursing, especially when the calves were over 1 week old. Older calves were traveling so rapidly and in such large, constantly mixing, groups that one calf could be observed for only a few minutes.

During 720 minutes of observation of calves under 2 days old 40 successful nursing events were observed, or one every 18 minutes. Since the average duration of a nursing event is 30 seconds, the chances of a calf being seen nursing in a one-second interval is approximately 1 in 36. Latitudinal counts were made by scanning groups with calves over 1 week old. In these groups only 1 out of 100 calves was nursing when observed. The time required to scan such a group was about 2 minutes, if the view was unobstructed. Thus within a one-second interval approximately 1 out of 100 calves was nursing. Therefore it appears that calves nurse only about one-third as often in their second week as in their first days of life.

The cow almost always ends a nursing event by moving away. Ninety events were terminated by the mother. The calf stopped nursing before any action by the cow in only 13 events. In four out of 137 events the nursing was recorded as being initiated by the cow. That is, some activity of the cow appeared to induce the calf to approach and nurse. In two cases the calf was resting and was nudged by the cow until it rose and started suckling. In the other cases the cow orientated itself so that the udder was at the calf's head. In all four cases the cow grunted to the calf.

On two occasions calves were seen to nurse successfully from cows that were not their own mothers. Both these nursings were from between the hind legs. After a few seconds the cows became aware that their own calf was not

suckling and chased the strange calves.

An additional behavior pattern often occurring during nursing is that of "bunting" (or "rooting") by the calves. These thrusting and pushing movements against the udder have been frequently observed in many ungulates, as well as other mammals, but to my knowledge there has been no detailed study of the phenomenon. Zaks (1962:86, English translation from the Russian) says the following on the subject:

It is evident additional mechanical stimulation of the gland causes further contraction of the alveoli which combines with the effect of oxytocin in ensuring that milk is drained as completely as possible and may even replace oxytocin under certain conditions.

Zaks goes on to say that the detailed study of this aspect of suckling is of great importance.

Bunting was recorded only 11 times in the systematic observations, but was also often observed in the course of other activities. Older calves show a greater tendency to bunt either before starting to suckle or during a suckling event. Only one calf under a day old was observed to bunt. Older calves may bunt so vigorously that the cow is pushed out of position. On several occasions bunting appeared to be painful to the cow and resulted in her moving away from the calf or, in the case of a few winter observations, directing agonistic acts towards her own calf.

During the collection of milk samples from dead cows (see below) it was found that more milk could be ob-

tained by punching the udder occasionally with a closed fist. Thus at least with dead cows the effect on milk letdown is a mechanical one, as Zaks (1962) states. Y. Espmark (pers. comm., 1962) reports that punching of the udder facilitates milk letdown in reindeer, also.

Milk samples were collected immediately after death from three caribou cows with calves under 1 month old. These samples were analyzed by Dr. R. Jenness of the Institute of Agriculture, University of Minnesota. The results of these analyses are shown in Appendix D along with some analyses of reindeer milk for comparison. The composition of the caribou milk analyzed by Dr. Jenness is similar to that of reindeer during the early stages of lactation. It is interesting that both Aschaffenburg et al. (1962) and Berge (1963) show an increase in fat and protein contents later in the lactation period of reindeer.

Head Bobbing

Pruitt (1960) describes five basic postures and actions serving as social releasers in caribou. He calls these "threat", "attack", "alarm", "excitation leap" and "head bobbing". I will deal with the first two of these under "Agonistic Behavior" and the "alarm" and "excitation leap" under "Reactions to Man". In addition another basic posture, the "attraction pose", is described later in this section.

Because head bobbing is of widespread occurrence in many aspects of caribou behavior and is especially import-

ant in the mother-infant relationship I shall consider this phenomenon before treating any further aspects of social behavior.

Pruitt has adequately described the head bobbing act. Fig. 5 from his paper (1960:12) is reproduced here (Fig. 10) to illustrate the action (see also App. A, Nos. 3 and 16). Pruitt (1960:11) states: "head is lowered so that muzzle nearly touches the ground (Fig. 5a), then head is returned about one-half to two-thirds of the way to full recovery and stops (Fig. 5b). Head then slowly resumes original position (Fig. 5c)." It should be noted that the neck is held straight or slightly curved convexly downward. In contrast, in the threat posture the neck is bowed upward and the forehead held perpendicular to the ground.

The head bobbing movements are of particular interest because they occur in so many different situations in caribou but are apparently lacking in the repertoire of other ungulates. According to my observations, head bobbing movements may occur in the following types of situations.

- 1) Upon confrontation with rivers, cliffs or embankments, zabois (deep, wind-deposited snow in depressions), ice, etc. - by all classes, but males only occasionally.

- 2) Upon alarm or suspicion when man, predators, or unusual objects (such as a tent flapping in the wind) are observed or when surprised by another caribou - especially by cows and immature individuals.

- 3) When attempting to elicit rising and/or following

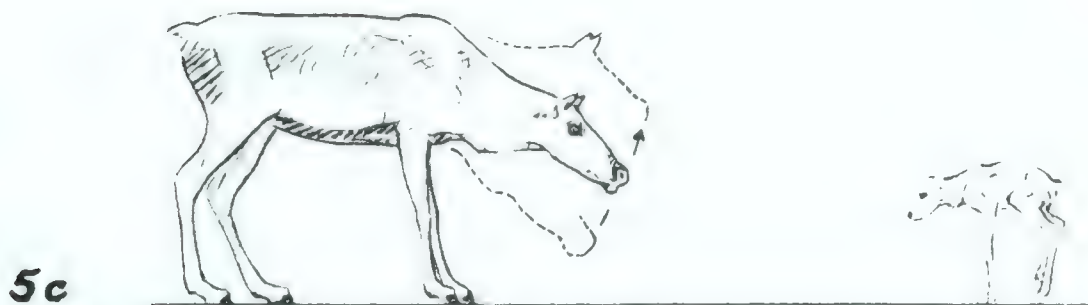
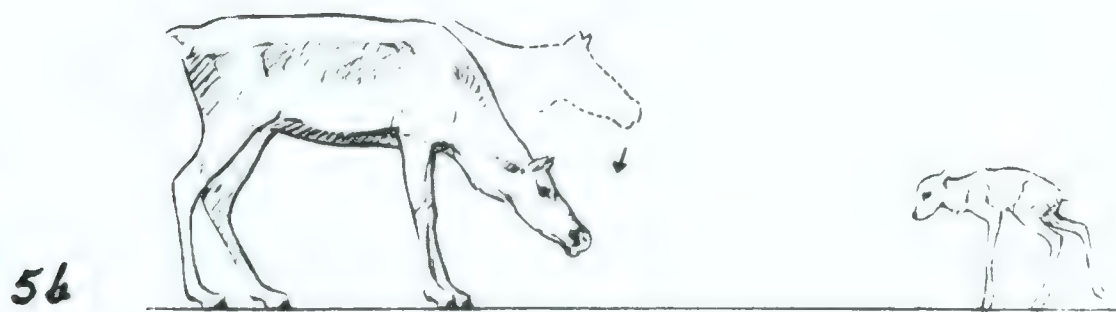
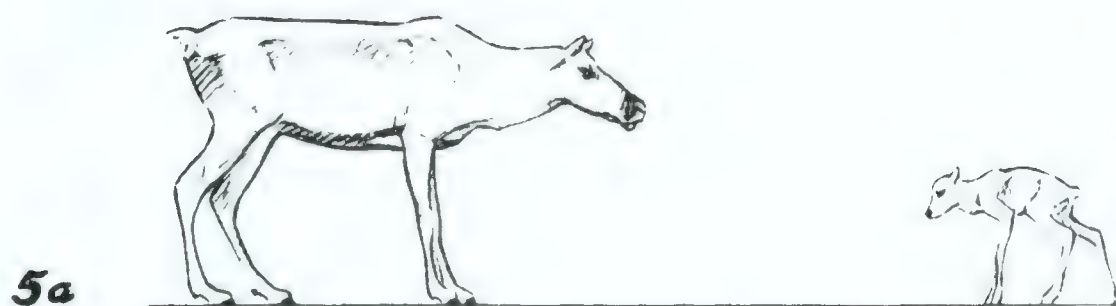


Fig. 10. Head bobbing by a cow to a new-born calf.
(Sketches by W. D. Berry, reproduced with
permission from Pruitt, 1960)

responses in calves - by mothers or less often by other cows.

4) When approaching other individuals, as when searching for mother, but only rarely to own mother - by young calves, and by other individuals approached by calves.

5) When adult individuals or groups of individuals meet - rare.

All the above situations, possibly excepting those of type 5, are ones in which the individual is presented with a conflict of "drives" (sensu Thorpe, 1963:15). In type 1, above, the "desire" to follow other individuals or continue in the direction of movement conflicts with the fear of the obstacle. For example, individuals encountering a high river bank may walk along the bank, occasionally approaching the precipice and head bobbing, until an easier spot for crossing is found.

In the second type of situation head bobbing is most likely to occur when the source of disturbance is not immediate or clearly defined, usually in the moment between the end of feeding activity and the beginning of fright or escape responses.

Situations of types 3, 4, and 5 usually involve social interactions although occasionally head bobs were undirected and often when directed at another individual did not elicit any overt response. Detailed descriptions were recorded of 64 events involving head bobbing. The class of individuals executing and receiving (if any) the movement and the circumstances in which it occurred are shown in Table 16.

Table 16. Recipients and circumstances associated with occurrence of head bobbing movements.

Head bobbing by calves		
Circumstances	Recipient	Number of Observations
During exploratory play	Undirected	2
When lost, separated from mother	Undirected	5
Standing near mother	Undirected	1
When approaching other calves	Calves	8
Following head bob by another calf	Calves	3
When approaching and investigating other individuals	Cows & yearlings	8
After receiving agonistic gesture	Mother	1
After series of rebuffs to nursing attempts	Mother	1
"Greeting" after long separation	Mother	<u>1</u>
	TOTAL:	30
Head bobbing by cows		
Circumstances	Recipient	Number of Observations
When meeting obstacles (Type 1 in text)	Undirected	5
When searching for lost calf	Undirected	3
Eliciting rising and/or approach responses	Own infant	11*
To attract, when infant is following another cow, or running away	Own infant	5
"Greeting" after long separation	Own infant	2
When approached	Calves (not own infant)	<u>4</u>
When attempting to elicit following, lure away from mother	Calves (not own infant)	<u>4</u>
	TOTAL:	34

* Frequently a long series of head bobbing bouts interspersed with other activity but here each series is considered as one event.

Head bobbing occurring in situations of type 5 is not included in the table. These uncommon occurrences were the only cases in which head dips were directed by one cow towards another.

The dipping of the head is a stereotyped motor pattern appearing during the first hours of life. The new-born calf often puts its head to the ground, even pokes it in the vegetation, during its first day without actually feeding. (Just as young passerine birds will peck but not swallow and rely upon gaping to obtain food; Hinde, 1953). Unfortunately, the possible significance of this action was not considered until the last summer of work, therefore no quantitative data were obtained concerning it.

Cows with newly-born calves are the individuals most likely to be presented with conflict situations. It is by such individuals that head bobbing is performed most frequently and apparently with the greatest intensity. (Intensity was not actually measured). The urge to flee from potential danger or to follow or join a group is continually being opposed by the urge to remain with the calf. Under such circumstances head bobbing serves as a signal, releasing a response in the calf. The efficiency of this releaser in mother-infant relationships cannot be overemphasized. Head bobbing by a mother was always observed to release at least an attempt to follow by her calf, except in a few cases where the calf appeared totally exhausted.

Play and exploratory behavior

Any discussion of "play" immediately encounters

difficulties of definition. Thorpe (1963) notes that there may be various possible explanations for behavior presently lumped under "play"; i.e., the category is an artificial one. In this study, also, several activities of uncertain significance are considered under the general heading of "play".

Thorpe (1963:95) considers true play to occur when the circumstances of the environment or life history are such that "appetitive behaviour becomes emancipated from the restriction imposed by the necessity of attaining a specific goal".

Shillito (1963) believes that much of the activity of young animals that has been called "play", based on the lack of a definite consummatory situation, could be described as simply exploratory behavior. She divides exploratory behavior into two phases: 1) reconnaissance behavior in the form of more or less random movements and, 2) investigative behavior directed towards specific objects in the environment.

Forty events involving calves during the calving and postcalving periods received a preliminary classification of "play". The types of activities occurring in these 40 events are shown in Table 17. Seventeen of these 40 events were referable to a generalized reconnaissance activity in which the calf left its mother on runs of varying length, apparently not directed towards any specific goal. In eight of these reconnaissance runs there occurred gamboling, bucking, and similar movements that are always associated with play in ungulates.

Table 17. Types of play and exploratory activity in calves less than 1 month old.

Type of activity	Number of observations
Lone reconnaissance activity	17
Lone play around mother	6
Play involving two calves	11
Play with mother	3
Play with yearling	<u>3</u>
TOTAL	40

In the three cases where calves directed gamboling and head bobbing movements towards yearlings, one resulted in an immediate fright and escape response by the yearling, the second in an antler threat followed by withdrawal of the yearling with gamboling motions, and in the third the yearling approached the calf which then took fright and returned to its mother.

In none of the events in Table 17 were there series of interactions involving young calves that might be called "games", such as Darling (1937) has described for red deer and Altmann(1958) for wapiti.

Only three interactions between calves and their mothers were called "play". In all three cases the calves rose on their hind legs and struck or rested their forefeet against the mother's body. It is likely that these actions were play mounting movements and not derived from the rearing associated with agonistic behavior. Mounting movements are performed by the calves of other ungulate species (Schloeth, 1958; Eygenraam, 1963; Marjoribanks Egerton, 1962).

One activity occurring in almost all phases of play and exploratory activity is flight, most frequently oriented toward the mother. This rapid return to the mother occurs at the end of most reconnaissance runs and after many encounters of calves with other individuals. Meyer-Holzapfel (1956) notes the widespread occurrence of flight and escape elements in the play of ungulates as opposed to the predominance of fighting and capturing play in predatory species.

In several of the runs there was no overt exploration of the environment. The calf merely ran out and immediately returned. Such cases appear as simple "exercising" or perhaps they aid in the development of the fright and following responses, as will be discussed later.

The exploratory runs of calves were seen as early as the first day of life in four cases. In these events the distance the calf traveled from the mother varied from 20 to 60 feet. In the days following the calves extended their runs to distances up to 200 yards, usually in the form of an extended "figure-eight" with the mother at the center of the figure. One calf, a few days old, was estimated to have traveled a total of 500 yards in one and one-half minutes while making "figure-eights" around its mother.

An identical exploratory activity has been described in the American bison by Marjoribanks Egerton (1962).

In nine of the 17 reconnaissance runs calves directed investigative behavior toward objects, seven towards other caribou, one towards water, and one, accompanied by pawing, towards a high tussock.

Reconnaissance behavior should not be confused with the searching behavior of young calves separated from their mothers. In the latter case the calves have a specific goal: reunion with the mother. On two occasions reconnaissance behavior was observed to result in separation in which the calves then showed typical searching responses.

The majority of cases in which calves showed

investigative behavior are not included in the 40 observations in Table 17. These cases include all those in which calves left their mothers and directly approached other individuals. The types of interactions resulting from these approaches and their significance are considered elsewhere.

Play between infants is limited both in frequency and duration. Only 11 events were classified as such play. Actions of an agonistic type occurred in five of these events: one antler threat posture by a 2-day-old calf, one antler threat and charge with hooking motions by a 1-day-old calf, and three events in which calves reared briefly and struck at each other with their forelegs. Two of these last three events are the only ones in which any actual calf-calf contact occurred. De Vos (1960) reports similar "boxing" behavior in the caribou calves he observed. The actions of all these calves in the play-agonistic events were similar to those of adults, except that they showed slightly poorer motor coordination. These actions are described on pages 93 and 94.

In eight cases calves approached other calves with frisking and gamboling movements typical of play. Occasionally their attitude conveyed to the human observer the idea that it was "inviting the other calf to play", but this invitation, if such it were, was not often accepted. Only two of the calves so approached reciprocated with brief play-fighting, all others avoided the approaching calf and most fled to their mothers. These avoidance reactions could not be distinguished from those occurring in other situations.

Agonistic Behavior

Pruitt describes and discusses two basic agonistic postures which he calls "threat" and "attack" (1960:9). I have modified the names he used for these postures and in addition describe three other movements important in agonistic behavior. For the two postures Pruitt calls "threat" and "attack" I have adopted the names "head-high threat" and "antler threat". These are the same terms used by Geist (1963) to describe the agonistic postures of moose (Alces alces andersoni), although the function of the postures is not identical in the two species. Nothing comparable to the "head-low threat" described by Geist was observed in caribou.

The five "social releasers" used in the agonistic behavior of caribou are described below.

Antler threat: The head is lowered almost to the ground so that the top of the head is perpendicular to the ground or bent slightly inward towards the front hooves. The back is hunched and forelegs are often held rigid and slightly spread apart (Fig. 11, also see App. A, No. 14). Charging towards the recipient may occur but since this "attack" element does not always occur nor is it limited to this act, I have avoided using the term "attack" that Pruitt used.

Both antlered and unantlered cows employ this posture and both hold their heads in a position which points the antler tines towards the opponent, or would if antlers were present. Antlerless cows strike opponents with the top of the head in "contact" events (see below).

This posture is similar to the "crouch" occurring in the agonistic behavior of Odocoileus hemionus columbianus) and illustrated by Cowan and Geist (1961), but the hunching of the back is more pronounced and the head is held at a lower level in caribou than in the deer shown in their illustration. Burckhardt (1958) also illustrates a similar posture (position d'intimidation) occurring in red deer.

Head-high threat: The rostrum is extended directly forward so that the top of the head is parallel or nearly parallel to the ground. The ears are laid back. The animal may advance towards the recipient directly or at a slight angle. In the case of cows, the neck is held straight, not to the side as by males in courtship display (see comparative figures in Pruitt, 1960:6).

Hooking: The head is lowered as in the antler threat but not as close to the ground. It is then swung upward and to one side in an arc. The points of the antler tines may make contact with the recipient but the act is not limited to antlered animals. The front legs are frequently spread apart.

Foreleg striking: One foreleg is lifted and jabbed in the direction of the recipient. The act is similar to the stereotyped digging motion (see Pruitt, 1960:18). The movement is always performed when the animal is stationary.

Rearing: The animal rears up on its hind legs with the forelegs more or less bent and hooves directed towards the recipient. (Fig. 12, see also App. A, No. 14). The posi-



Fig. 11. Antler threat by one cow towards another.



Fig. 12. Two cows rear and strike at each other.

tion is held for only a second or two by adults, but calves were observed to rear up and remain so, "boxing" with each other, for up to 30 seconds in "play-fighting". Darling (1937) shows this act occurring in red deer.

On one occasion a cow was observed to put its weight on its forelegs and kick backwards with the hindlegs at a strange calf.

In the description and discussion that follows reference is made only to the agonistic behavior occurring in the period from mid-May to early July, including the early postcalving period, and not to agonistic behavior associated with the rut or with winter competition. During the 4 years of work in this May-to-July period detailed notes were taken on 134 events involving agonistic acts. The data are not complete for all 134 observations, thus some points in the discussion are based on somewhat fewer observations, as noted. Cows were the executors of all agonistic acts in the period considered here except for four acts by yearlings towards calves and two acts by bulls towards yearlings.

The proportion of the total observations contributed by each of the five types of agonistic releasers is shown in Fig. 13.

As I have mentioned, agonistic acts sometimes include movement towards the recipient. The proportion of acts of each type in which there was rapid movement ("charging") towards the recipient is also shown in Fig. 13. "Charging" occurs most frequently in combination with head-high threat

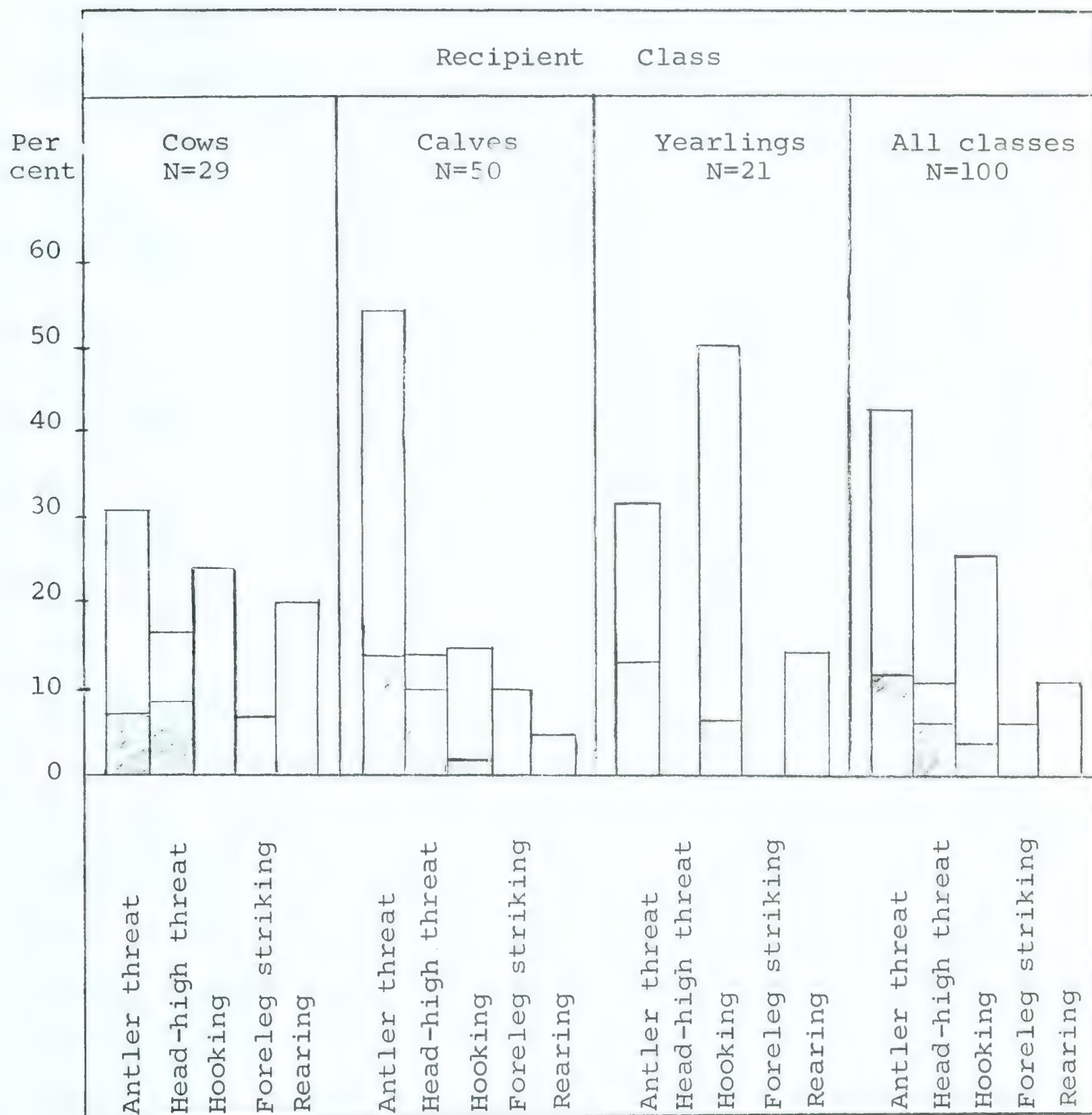


Fig. 13. Comparison of proportions of different agonistic acts directed by cows towards cows, calves and yearlings. (mid-May to early July)



Proportion of all types accompanied by charging.

(7 out of 12 times). Head hooking was occasionally preceded by charging. The proportion of antler threats accompanied by charging was low (12 out of 44 events).

I recorded the recipient of each agonistic act as either calf, yearling, cow or bull. Only two observations were made in which bulls were the recipients and these are not considered here. Fig. 13 shows the proportions of the total agonistic acts directed towards each class made up by the different agonistic postures. It may be seen that the postures were not directed with equal frequency to the three recipient classes. The differences between the classes were tested with simple "2 x 2" contingency tables and showed some significant associations between acts and classes of recipients.

The antler-threat predominates among the postures directed towards calves and occurs in a significantly greater proportion of the acts ($.02 > P > .01$, Table 18a) towards calves than towards yearlings or cows. "Hooking" acts comprise a larger proportion of the agonistic acts directed towards yearlings than towards cows and calves ($P < .01$, Table 18b). There is no single agonistic act directed significantly more frequently towards cows alone, however, "rearing" composes a greater proportion of the acts directed toward cows than towards calves ($.02 > P > .01$, Table 18c). The greater proportion formed by head-high threats in the acts directed towards cows than towards the yearling class is of doubtful significance ($.10 > P > .05$, Table 18d) and the absence of foreleg striking in the acts directed towards yearlings is not significant ($P > .10$).

Table 18a-d. Tests of the association between certain agonistic acts and recipient classes.

	<u>Recipient</u>	<u>Agonistic Acts by Cows</u>	
		N=	N=
<u>18a.</u>		Antler-threat	Others
	Calves	28	22
	Others	16	34
		$\chi^2 = 5.9$.02>P>.01	
<u>18b.</u>		Hooking	Others
	Yearlings	11	10
	Others	15	64
		$\chi^2 = 9.6$ P<.01	
<u>18c.</u>		Rearing	Others
	Cows	6	23
	Calves	2	48
		$\chi^2 = 6.4^*$.02>P>.01	
<u>18d.</u>		Head-high	Others
	Cows	5	24
	Yearlings	0	21
		$\chi^2 = 2.9^*$.10>P>.05	

* Calculated using Yate's continuity correction.

Table 18e, f. Tests of the association between the frequency of occurrence of certain agonistic acts and the period of observation.

	<u>Agonistic Act</u>	<u>Period</u>	
		N=	N=
<u>18e.</u>		Precalving	Calving
	Antler-threat	3	33
	Others	14	28
		$\chi^2 = 5.8^*$ $.02 > P > .01$	
<u>18f.</u>		Precalving	Calving
	Rearing	7	3
	Others	10	58
		$\chi^2 = 10.0^*$ $P < .01$	

Table 18g, h. Tests of the association between the frequency with which agonistic acts are directed towards certain recipient classes and the period of observation.

	<u>Recipient</u>	<u>Period</u>	
		Calving	Postcalving
<u>18g.</u>			
	Cows	6	14
	Yearlings	7	11
		$\chi^2 < 1.0^*$ $P > .10$	
<u>18h.</u>		Calving	Postcalving
	Calves	39	13
	Others	22	38
		$\chi^2 = 16.5$ $P < .01$	

*Calculated using Yate's continuity correction.

Observations were classified according to the period in which they occurred as follows: 1) Precalving - observations on the calving grounds but before the beginning of calving or of groups without calves, early in the calving season. 2) Calving - observations during the calving season mainly of interactions occurring in nursery bands. 3) Postcalving - observations of interactions in the large aggregations that form at the end of the calving season, and in the 2 weeks following the end of the calving season. Fig. 14 shows the proportion of each type of act in the observations for each of these periods. The sharp rise in the proportion of antler-threats in the calving period and the decrease in the proportion of rearing acts from the precalving to the postcalving period are both significant ($.02 > P > .01$, $P < .01$, Table 18e,f). Because of the small number of observations in the precalving period (when no calves are present), the proportions for all recipient classes combined (Fig. 13) are subject to some distortion. During the calving and postcalving periods the proportion of calf-directed acts was even more predominant than is indicated by the number of observations shown in Fig. 13. The change in the ratio of cow-directed to yearling-directed acts between the two time periods is not significant ($P > .10$, Table 18g). The difference in the proportion of calf-directed acts in the calving period (39 out of 61) compared to the postcalving period (13 out of 51) is highly significant ($P < .01$, Table 18h). This decrease in the proportion of calf-directed acts in the postcalving period was recorded in

Per cent

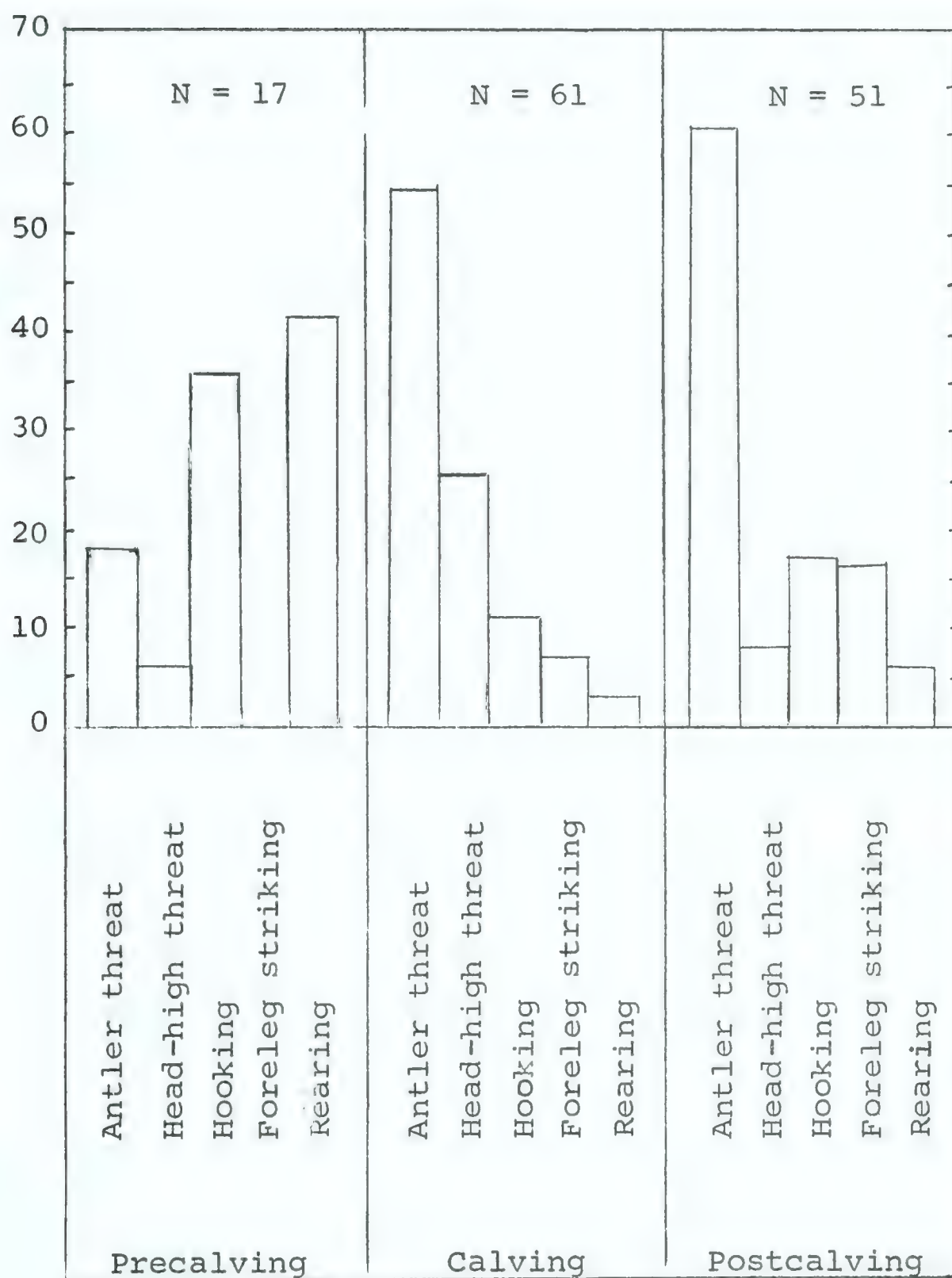


Fig. 14. Proportion of five types of agonistic acts in each of three periods, Mid-May to early July.

spite of a slightly higher average proportion of calves in the groups observed after calving. The decrease is explained by the improved ability of calves to recognize their own mothers and to distinguish and avoid other classes of individuals. In addition, these other classes, particularly the cows accompanied by calves, show greater tolerance towards calves after the end of the calving period.

Actual contact between individuals occurred in 17 out of 134 events (13 per cent). The types of contacts observed and the recipient individuals are given in Table 19. In 15 of the events the "executor" (the animal directing an agonistic act toward another) was a cow or, in the case of simultaneous rearing and head-to-head contacts, at least one member of each interacting pair was a cow. The other members of these pairs are given in Table 19.

Since all but 6 of the 134 events were executed by cows (4 by yearlings, 2 by bulls) the class of executing individual was not considered as a significant variable in the analysis of acts presented above. On 35 occasions the cows executing agonistic acts could be definitely classified as "accompanied by calves". The recipients of these 35 acts are shown in Table 20. There was no significant difference in the proportions of these acts directed towards the three classes by mothers compared to the proportions of these acts directed by all cows in the calving and postcalving periods. However, a slightly higher proportion of the acts by mothers were directed towards calves and it is possible that if all

Table 19. Types and recipients of agonistic acts involving actual contact.

Type of act	No. obs.	Recipients
Antler-threat to body	7*	Cows - 5, yearlings - 2 (from bulls)
Head to head contact	3**	Cow with cow - 1 Cow with yearling - 1
Hooking to body with antlers	2**	Yearlings
Striking with foreleg	3**	Calves, 1 from own mother
Rearing and striking with hooves	2**	Cows
* 3 by antlered cows, 2 by unantlered cows, 2 by bulls, antlers in velvet		
** by cows		

Table 20. Frequency with which different classes of individuals served as recipients for agonistic acts by cows with calves.

Recipient class	No. obs.	Per cent
Cows	8	23
Yearlings	6	17
Cows' own calves	3	9
Other calves	<u>18</u>	<u>51</u>
TOTAL:	35	100

the mothers could have been positively identified this difference might have proven significant. During observations of moving groups it was not always possible to identify an "aggressor" cow as "mother" or "non-mother".

Fright and Escape Reactions to Man

The fright and escape reactions of caribou are necessarily described from observations of their reactions to man. The limited number of observations of their reactions to predators and other species are considered separately. There is no indication that the basic acts involved differed according to the species causing the alarm.

Although the reactions of caribou to man are the most easily observed elements of their repertoire of behavior, they also proved to be difficult to analyze. The number of variables influencing the fright and escape behavior is very high and much of the variability in the caribous' reactions still cannot be adequately explained. As might be expected, the reactions of caribou to man are also the phase of their behavior most frequently described in print. Every Arctic explorer seems to have had a few remarks to make on the subject. Only a few of the more explicit observations from reliable sources are cited here and in the subsequent discussion.

In my own notes there are approximately 150 descriptions of events in which caribou reacted in some way to me or to other humans. While the majority of these events were occasioned accidentally, others were planned intentionally

to attempt to isolate some of the variables influencing reactions to man. In addition, McWilliams, Kantner and Lønø provided many observations on the behavior of cows and calves observed during the calf-tagging program. During the program of specimen collecting that was carried out for "Project Chariot" there were many opportunities to observe the reactions of calves of different ages after their mothers had been killed.

Most of the basic acts and social signals occurring in fright and escape reactions may be seen at all times of the year. Therefore, a more general discussion of these acts is required before considering the reactions of cows with newborn calves. Since the reactions of these cows and their calves include behavior patterns not seen at other times these are treated separately below. Further remarks on seasonal changes on reactions to man may be found in Section 8.

The act most frequently occurring when a caribou is frightened, but before it flees, is the "alarm pose". Pruitt (1960) describes it as a ritualized pose derived from the normal stance used during urination and defecation. Urination itself occasionally occurs when an individual is frightened. In the pose, one hind leg is extended out to the side in an exaggeration of the urination pose. This act is illustrated by Pruitt (1960:40) and on the front cover of Harper's publication (1955), and is shown here in Fig. 15 (see also App. A, Nos. 13 and 23). The alarm pose is a social



Fig. 15. Urination pose. (Alarm pose)

releaser. It produces an alert state in other caribou viewing it and they orientate themselves in the same direction as the releasing individual. Grunting occasionally accompanies the alarm pose, especially in the case of cows with calves.

While the pose is taken most often as the result of some disturbing visual stimulus, it has also been observed in response to the scent of humans. In these latter cases the animal usually stands with its head pointing downwind. Head bobbing and "scenting" motions are more likely to occur in response to strange odors.

Although the alarm pose stimulates alertness in other members of a group it is not by itself sufficient to initiate escape reactions in these individuals (except possibly in some cows with young calves). The flight of the individual executing the alarm pose, or the perception of the source of alarm by other members of the group must provide an additional stimulus before the group will flee.

Tail erection accompanies the alarm pose and flight, but I have no evidence that erection of the tail alone may act as a releaser. It did appear on several occasions that an alert stance by one caribou, that is, a posture in which the animal stares fixedly with its tail raised and head up, was sufficient to attract the attention of other caribou in the absence of the alarm pose.

Another social releaser, the "excitation leap", was first described by Dugmore (1913). It is a behavior pattern of particular interest because of its unusual nature. As

typically performed by a bull, the act consists of raising up high on the hind legs, and at the same time pivoting part way around, before fleeing from a source of alarm (see illustration in Pruitt (1960:16)). Dugmore believed that a drop of fluid was ejected from the interdigital glands of the hind feet during this act and Pruitt (1960) observed separation of the hind toes in the tracks left by bulls performing the excitation leap. He describes the odor as being "reminiscent of the smell of fresh Populus bark and sap or possibly similar to phenol" (Pruitt, 1960:15).

The observations of Dugmore and Pruitt and my own are all in agreement that something is left on the ground during the excitation leap that can elicit a fright response in a caribou crossing the spot sometime later. It is not necessary for this following individual to see the releasing animal or any source of alarm. Although Quay (1955) found that the interdigital gland is equally developed in both sexes, all observers also agree that the act is most commonly executed by mature males. It is also frequently performed by yearlings and I have observed a full excitation leap by a 4-month-old calf (App. A, No. 11).

In addition to this full excitation leap, in which the body axis may rise 70 degrees above the horizontal, there also occurs a high bounding movement, in which the body does not rise so high and the pivoting motion on the hind feet is slight or absent.

No clear distinction between these two motions is

found in the literature. Murie (1935:33) evidently noted that the pivoting does not always occur, for he speaks of a "spy hop" in which the caribou "sometimes pivot part way around". Harper (1955) describes under the topic of "Gaits" the initial leap caribou often make when frightened in which, he notes, all four feet may leave the ground. Harper does not describe any variation in the leaping. I observed some intermediate movements that could not be definitely classified as either a true excitation leap or as bounding.

Bounding, as a fright reaction, occurs in several species of antelope inhabiting grasslands. Brooks (1961) refers to "spronking" by Thomson's Gazelle (Gazella thomsonii). The bounding trait is most highly developed in the springbuck (Antidorcas euchore) and the impala (Aepyceros melampus) (see Wynne-Edwards, 1962). The bounding of caribou is never of the magnitude seen in these species, neither in the height or duration of the bounds. Nor does it have the "contagious" effect that is seen in other species. With regard to caribou, it is impossible to say whether "bounding" is an alarm signal that stimulates other caribou to take flight any more readily than they would simply at the sight of another animal running.

According to an informant quoted in Harper (1955) it is usually a single animal that leaps so, but the informant had observed as many as six together leaping into the air. I also concluded that single animals, or at least individuals not in compact groups, showed a greater tendency towards "bounding", and cows with young calves showed a particular

propensity to do so. Further description of this bounding behavior is presented in connection with the reactions of mothers.

The pedal, or interdigital, glands, from which the scent is exuded during an excitation leap, occur in many other ungulate species as well (see Pocock, 1910, 1923). Nichol (1938) describes how white-tailed deer use the scent emitted from the pedal glands to follow other individuals or to backtrack themselves. According to Talbot and Talbot (1963) the scent left by the pedal glands of the wildebeest is so strong that a man is able to track them by it. However, I know of no other ungulate in which the use of a pedal secretion as a danger signal occurs.

It would appear to be in keeping with the more specialized function of the pedal glands in caribou that they occur only on the hind feet, whereas in other Neocervinae (Odocoileus, for example) the glands are present on all four feet (Pocock, 1923). Furthermore, Pocock says that according to Caton (specific reference not stated) some glandular material is present in the front feet of caribou calves, but is entirely gone later in life.

The potential value of such an olfactory danger signal in caribou is clear. Dugmore (1913) describes how migrating caribou will normally follow exactly in the trail of those preceding them, even though these leading individuals are out of sight. This trailing tendency is most marked on a soft or snow-covered surface. Under such conditions I have

observed that the scent left on the trail following an excitation leap not only causes the animals following to become more alert but can result in the formation of a detour around the location. Two examples of this detouring effect are depicted in Fig. 16.

If the lead individuals pass through undisturbed then those that follow along their trails will be less alert. Many hunters have recognized the value of letting the leading individuals in a large caribou movement go by. Dugmore (1913) believed that once a trail was established the animals following felt secure. Ingstad (1954) reported similar beliefs among the caribou hunters of Anaktuvuk Pass and I also have heard the opinion expressed by experienced Eskimo hunters that the leaders should be allowed to pass by unmolested. It may be that the communicative role of the scent is important in the basis for these beliefs.

The "flight distance" of caribou may vary from a few feet to half a mile. Like Pruitt (1960) I was once able to stand in the cover of some bushes and reach out and touch a caribou on the rump as it went by. This animal started slightly but then continued slowly on its way. At the other extreme, a cow about to give birth reacted to movement by me when only my head was visible at a distance of over 500 yards.

Kelsall (1957) considers 100 yards to be a typical flight distance but he also emphasizes, more so than previous writers, the great variability in the reactions of caribou, and gives many examples of both extremely short and extremely

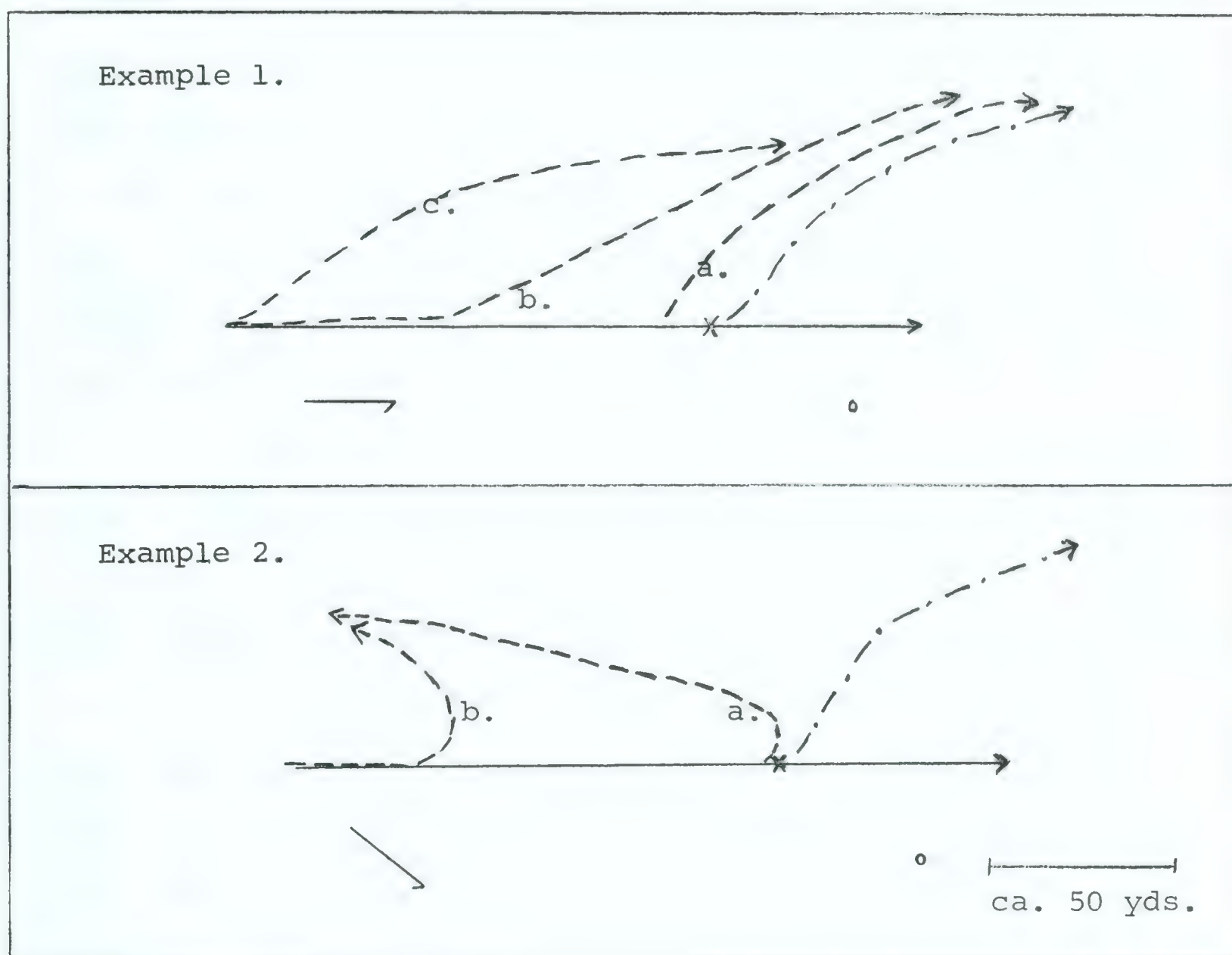


Fig. 16. Two examples of the effects of excitation leaps on following individuals.

x Location of excitation leap o Observer (source of original alarm)

———— Path of leaders
 - . - . - . Path of individual after giving excitation leap
 - - - - - Detoured paths of following individuals

a. = Individual reacting to scent left by excitation leap

b. and c. = Individuals reacting to sight of individual "a" fleeing

————> Wind direction

long flight distances in caribou he observed.

Murie (1935), Kelsall (1957) and de Vos (1960) all comment on the curiosity of the caribou. The trait is shown most strongly in yearlings and 2-year-olds and least in cows with calves. De Vos (1960) describes how a kicking motion of a man's legs in the air may attract a caribou to within 50 feet of the performer. Much of this curiosity or investigative behavior seems directed at confirming some impression received via one sensory mode by another mode.

Kelsall (1957) shows diagrammatically the investigative behavior of several caribou bands. I agree with his observation that such behavior is most common in late winter and spring. Typically, an investigating group will flee downwind after circling the observer, and show a characteristic "zig-zag" retreat, occasionally stopping to look back (Fig. 17). The common occurrence of head bobbing movements during this approaching and circling behavior has been noted elsewhere.

The Fright and Escape Reactions of Mothers and Their Young Calves.

The behavior of a frightened mother varies according to the age of her calf and the proximity of the source of alarm. When a cow with a neonate calf becomes suspicious it will normally move to its calf and induce it to follow by head bobbing, soft grunting, or occasionally by nudging the calf. Then the mother moves away from the source of alarm. If the calf is not able to travel rapidly she will return to it

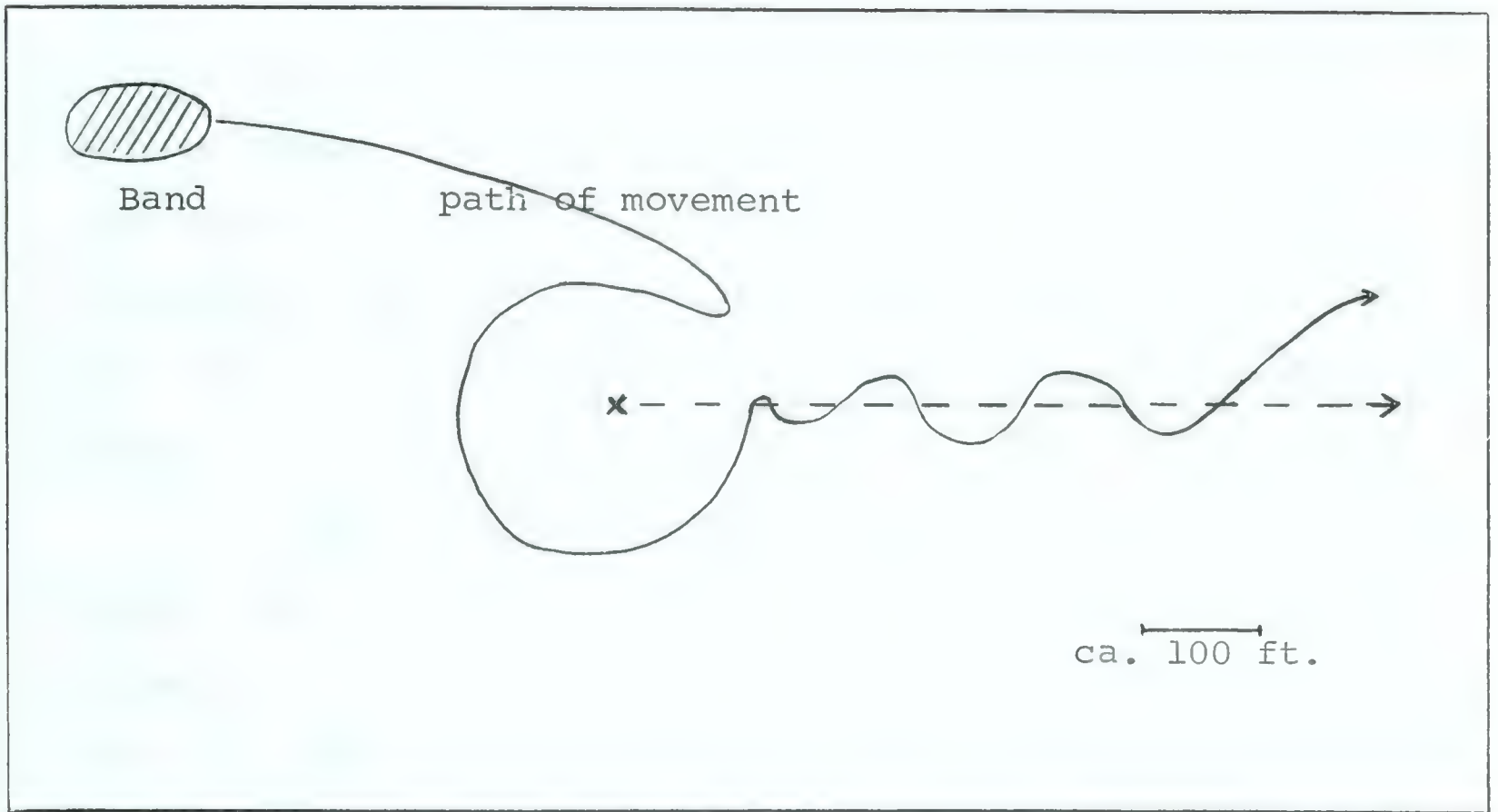


Fig. 17. Typical investigative and fleeing movements of a caribou band.

X = observer

-----> "Scent path" from observer

frequently, head bobbing, and otherwise inducing it to follow. In one case a cow started out and returned to her calf 9 times in 3 minutes. The calf was only able to travel about 50 yards in those 3 minutes.

If the cow and calf are in a group with few or no other cow-calf pairs, they may leave the group when disturbed without the others being alarmed. Or, if the others are acting nervous and alert, the cow may lead her calf away without actually observing any external source of disturbance. In nursery bands, where almost all the individuals are cows with calves, their flight will normally induce the few others present to follow.

One of the most consistent behavior patterns in the escape reactions of cows with young calves is a movement up-slope when frightened. This striking habit was noted separately by both McWilliams and me in 1960. McWilliams described in his field notes (May 29, 1960) a group of six yearlings, eight cows with calves and four other cows. When chased, the cows with calves split away from the rest of the group. He wrote: "the striking fact was that the cows with fawns went straight up the ridge and the last few hundred feet were very steep and snow-covered; the fawns experienced much difficulty, slipping and sliding before they got over the top." The rest of this group fled following the contours of the hill.

I recorded on ten different occasions such a splitting up of groups where those cows with calves moved directly uphill when frightened. One of these observations was in the

first week of July when the average age of calves was about 1 month. This trait was not observed later in the summer. Lone cows with calves also showed a tendency to seek higher elevation when disturbed. De Vos (1960) noted that cows with calves tended to separate from other individuals and flee farther when disturbed but he does not mention the tendency to seek higher elevation.

When a source of alarm is close and approaching rapidly the reactions of a cow are more intense. She immediately attempts to initiate a following response in her infant. If she is chased and the calf is able to follow, the cow will move in front of it and pace herself at about the maximum speed the calf is able to maintain. Cows show widely varying success in pacing themselves. Many will speed 25 yards or more in front of the calf only to turn around, return to the calf and head-bob towards it. An increase in the speed of the calf is frequently seen following such head bobbing. Some cows are very adept at maintaining a distance of only a few feet in front of the calf, providing a constant strong stimulus for the following response (see Section 8).

If the calf fails to maintain speed and the chaser is getting closer, the cow may use one of two other behavior patterns. The first is a form of the attraction pose described in further detail later in this section (Fig. 18). The cow moves along side of the calf and slightly to the rear, or even directly behind it. She then holds her neck extended with the head at the same level as the calf's. The cow grunts

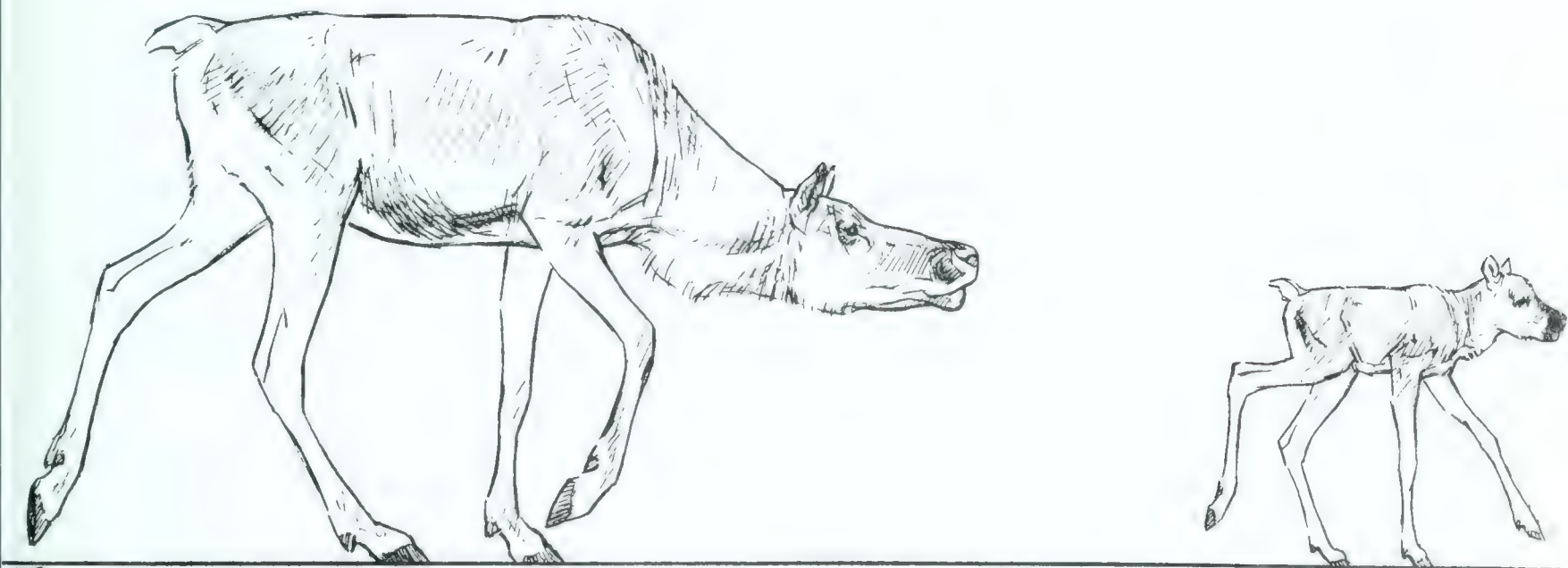


Fig. 18. Attraction pose. Shown here as it is performed by a mother from behind her calf when inducing it to run or cross a river.

continually and may nudge the calf, especially if she is running behind it. This behavior pattern is identical with that used by cows attempting to induce calves to cross rivers.

I have not observed the second behavior pattern which may be used under these circumstances but it was described to me by O. Lønø. This behavior was observed only when the calf stopped completely. The cow ran back and stopped a few feet in front of the calf then lay down facing it with her muzzle pointed towards it. After a few seconds she rose and again moved forward. In two out of three observations the calf made renewed efforts to rise and follow after this behavior.

If the calf was a neonate and unable to travel any appreciable distance, the cow normally remained near the calf long after other individuals had fled from the source of alarm. On some occasions she would repeatedly run up to the prone calf and head bob towards it or put her head directly to it. In spite of the stimulus thus provided many calves were unable to rise and follow at all. Other mothers never approached their helpless calves directly but circled them in an arc or complete circle at a distance of from 10 to 50 yards while the chaser approached. Cows exhibited a peculiar gait during this circling and when they fled from the chaser. Their movement is springy, showing more vertical movement of the body than normal, and the head is held high and extended forward with the rostrum parallel to the ground. The taggers were often able to identify cows with neonate calves by this

gait, although the calves could not actually be seen. Kelsall (1960:43) felt that some cows made an "... effort to distract attention by dashing wildy about close at hand."

In almost all cases once the chaser reached the location of the calf the cow either moved away slightly and continued to circle and run back and forth within about 100 yards, or she fled altogether. Three exceptions to this normal behavior should be noted, however.

On two occasions Kantner was charged while attempting to tag a calf. One cow charged him three times with her head in the antler threat position. These charges were accompanied by hoarse grunting. On the second occasion Kantner was charged so closely that he deemed it advisable to retreat and the cow was able to reclaim her rested calf and flee. Kantner noted on this occasion that if he sat down the cow acted frightened but as soon as he stood up it returned aggressively.

On one occasion when I had run down a 2 or 3-hour-old calf and had induced it to follow me, the cow returned and persistently ran up to within 10 feet of the calf and me, grunting loudly. Eventually I was discouraged from further experimentation and the calf immediately followed its mother.

Some cows abandoned their calves and moved off to a distance before the chasers had reached her vicinity. Some of these showed no circling behavior and, in fact, made no attempt to induce following in their calves. This does not imply that these calves were deserted, for often these same

mothers were most persistent in searching and relocating their calves after the intruders departed.

Why some calves were left behind and others were induced to follow until they collapsed is not clear. Both the age of the mothers and of the calves might have some relation to this difference but no consistent relationship could be demonstrated. Kelsall (1960) believed that older cows are more persistent in remaining near their calves.

With regard to the age of the calves, it was observed that some of the calves that were left by their mothers without hesitation were capable of traveling long distances. For example, McWilliams reported two calves that were left by their mothers while the taggers were still more than a quarter-mile from them. Both of these calves were several hours old and were not at all exhausted when found. They were located purely by chance as they lay motionless in the vegetation.

A low excitation leap ("bounding") was observed at the moment a cow left her calf on most occasions. In a snow squall in May, 1962 I had under observation two cows with calves off by themselves. One calf was under 2 hours old and obviously had not left the spot where it had been born. The other was somewhat older, but not over 4 or 5 hours. I decided to see what reaction I would cause by standing up suddenly at a distance of 150 yards. Both cows immediately gave bounding leaps and moved out of sight in the falling snow. The calves remained motionless. One of them was very conspicuous since

it lay on a surface of unbroken snow.

Although the excitation leaps or bounding occurred in the majority of cases when a cow left her calf, I was unable to determine if the leap had any signal function in such circumstances (see discussion, Section 8). The possibility was considered that the cow might leave a scent that would induce the calf to remain motionless. However, as I have already mentioned there is often little or no twisting of the hind hooves in these bounding movements by cows. I was never able to detect any odor. Furthermore, there were occasions when the calf remained motionless although the departing cow gave no bound, and there were a few cases in which the calf followed even though the cow bounded away. In these latter cases the calves that followed were over 1 day old.

De Vos (1960) states that caribou cows do not cache their young calves for long periods of time as do many cervids. It is true that the cows do not leave their calves for long intervals while feeding. It also appears that the caribou calf is in general far more active in its first days than the young calves of other cervids. However, de Vos also states that caribou calves show no "freezing" behavior pattern. With this I disagree. Although their performance is less consistent than that of red deer or white-tailed deer calves "freezing" responses do occur during the first 2 days of the caribou calf's life.

A motionless caribou calf can be extremely difficult to see. Its coloration blends well with the browns of the

tundra at that time of year. On several occasions calves were seen to lie down at a distance of 75 to 100 yards but upon reaching the spot the chasers had difficulty locating them. McWilliams noted one case in which a calf disappeared in the tussocks 25 yards from him and he was unable to locate it. When closely approached calves usually remained motionless except for twitching of the ears and nose, and eye movements (App. A, No. 4).

After they were handled, during tagging, the behavior of the calves again showed great variability. Most often, the calf rose and attempted to follow the taggers (Fig. 19). But others, especially older ones, showed slight avoidance movements (App. A, No. 4) and a few returned to a motionless posture. This latter behavior occurred in the extreme in one individual, 3 to 4 hours old, that remained completely limp while handled and lifted off the ground and was immediately motionless when released. Only its ears and eyes showed its alert state. When I imitated the grunting of a cow its ears tilted forward but there was no other reaction. The mother returned 15 minutes after I moved away and the calf immediately rose and followed her.

On three occasions calves that had not been handled responded to grunts and head bobbing motions that I directed towards them by rising and following. In two other cases calves followed when I walked near them but did not handle them or carry out any specific activity to induce following, other than merely walking.



Fig. 19. Tagged calf follows a man after being released.



Fig. 20. Caribou playing and resting on aufeis,
early July.

Although some calves, particularly the older ones, showed avoidance responses and struggled somewhat when being tagged, none showed a concerted escape response for more than a few yards. The significance of this is considered further in the discussion on the ontogeny of the calf's behavior (Section 8).

The largest calf tagged (25 pounds) showed avoidance responses and remained 25 feet away from the taggers until it was surrounded and "tackled". However, after being tagged and released, this calf followed a short distance behind the taggers until reclaimed by its mother.

The persistence of cows in locating and reclaiming their calves after they had been separated from them by the taggers has been described in detail by Lent (1961). One or the other of two conditions appeared to account for most cases in which cows failed to reclaim their calves. Either the calf was so young at the time of separation that the cow had not had sufficient time to identify herself with it, or frequent human activity around the area of separation discouraged the cow from returning and staying long enough to locate the calf.

On the basis of the tagging operations it was estimated that an undisturbed period after birth of at least half an hour is necessary to insure the return and searching activity of the cow. This estimate is similar to that given by Blauvelt (1954) as the time necessary for a goat mother to establish a strong enough bond with her kid so that she will not reject it after several hours of separation.

Ponomarev (1938) reported that abandonment of newborn reindeer calves most frequently occurred when herds were unexpectedly disturbed and that the majority of abandoned calves belong to yearling mothers.

During our tagging operation large nursery bands were sometimes taken by surprise so that several calves were simultaneously separated from their mothers. After the taggers withdrew the cows would return and search for their calves. McWilliams observed that a cow would normally stop a few feet from a calf and smell and examine it from there. Then one of two reactions would follow, either the cow would go up and make contact with the calf, leading it away (presumably having located its own calf), or it would react with fright to the calf. The reaction in this latter case would include excitation leaps, snorting and running from the calf. Cows were seen to react in this way to two or three calves before finally accepting one. It is possible that the human odor left on these calves, together with the odor of a strange calf, caused the observed fright reactions, but certainly the odor and sight of a mother's own calf was sufficient for her to immediately accept it, regardless of any possible human odor.

Reactions to Other Species

On five occasions grizzly bears (Ursus arctos horribilis) were observed to chase caribou and on two of these attempts they were successful in catching a calf. In eight other observations grizzlies were seen in proximity to caribou

but did not chase them. Ten observations were also made of bears feeding on caribou carcasses.

One of the calves was taken when a grizzly surprised a nursery band of about 80 cows at a river crossing. The behavior of the group was identical to that described by Lent (1961) occurring when a large band is surprised by taggers. Most of the calves were separated from their mothers during the crossing and this fact made it easier for the bear to run down a calf.

The other successful grizzly was observed to chase a group of six cows with calves for approximately 1 mile. Most of this distance the bear was only 50 yards behind the caribou. When nearly out of sight of the observer it finally caught a calf, which it appeared to devour on the spot. During the chase the bear passed within 50 yards of other caribou but ignored those individuals, which in turn, ignored him.

However, on most occasions caribou reacted to grizzlies by fleeing even though the bear showed no interest in them. The persistent efforts of the bear described above were unusual and in all the unsuccessful attempts that were observed the bear gave up within a few hundred yards. There is no doubt that the adult caribou is easily able to outrun a grizzly. On one occasion a badly crippled adult was observed to outrun a bear.

Wolves were uncommon on the calving grounds and winter range of the study population because of the activities

of bounty hunters. Thus few observations were possible. The observations made by the Crislers (1956, 1958) in northwestern Alaska and A. Murie (1944) are still the best available on this topic. It is interesting that Crisler (1956) observed that wolves had the greatest success in catching calves when they caused confusion in large groups. This is the same technique used successfully by taggers in catching younger calves (Lent, 1961).

Makridin (1962) has made some interesting observations from a helicopter on the speed of wolves and reindeer. The wolf is able to reach a slightly greater speed (53 mph, as opposed to 50 mph for the reindeer) but the reindeer has greater endurance. He states that the wolf will give up if it does not overtake its prey in 150 to 300 meters.

Both red and arctic foxes (Vulpes fulva and Alopex lagopus) were frequently seen on the calving grounds. The arctic foxes were present in especially large numbers in 1961, apparently because of an influx from the coast. Foxes were seen in the midst of caribou groups on seven occasions. Only once did the presence of a fox (red) cause widespread alarm and the flight of a group. In this case the alarm was started by one cow with a calf that ran from the fox. Although mothers with young calves were observed to act warily and nervously in the presence of foxes, no fox was seen to show any interest in even the youngest of calves. Both Stefansson (1921) and Harper (1955) gave accounts of caribou appearing to play with foxes.

Caribou were seen on a few occasions to stare at large birds. One cow with a calf a few hours old made head motions similar to hooking, and presentation of the forehead directed towards two low-flying jaegers (probably Stercorarius longicaudus) that circled her. In July, 1960, two golden eagles, (Aquila chrysaetos) were observed swooping low over a group of caribou and causing the animals to scatter, running wildly. The cows with calves moved to higher elevation. Kantner observed a young calf watching the flight of a bird. Only on one occasion did a group of caribou react to the alarm cries of a bird frightened by my presence. A group over one-quarter of a mile from me took flight when a bar-tailed godwit (Limosa lapponica) circled over me and screamed loudly.

Other Aspects of Maternal Behavior in Calving Groups

In previous sections we have seen that the young calf is often separated from its mother. Such separations may arise from the activity of the calf itself, as during reconnaissance runs or when it moves towards another individual. Separations may result also from the activity of the mother as when she leaves the calf in fright, or simply moves away from it to feed or follow other caribou. Finally, separations may result from another cow attracting a calf away from its mother.

During its first day the calf shows little discrimination when separated and will often attempt to associate with other individuals. Even at a later age it will attempt to associate with individuals which it recognizes as not being

its mother. This is demonstrated by several observations of calves following other individuals in the groups that immediately sought out their mothers when the groups were disturbed but had not yet started to flee. Thus the task of maintaining the social stability of the group falls mainly on the mothers. As will be described below, they act not only to maintain the bond with their own calves but also to reinforce the bonds of other cow-calf pairs.

Some of the activities of mothers that aid in maintaining social stability have been described. These include head bobbing and other actions to maintain the calf's following response, agonistic acts towards strange calves and other individuals, avoidance of strange calves, the use of attraction postures and grunting to regain control over their own calves, and searching activities when separated from their calves. The orientation of their feeding movements around the young calf is also of importance.

It has been shown that calves are the most frequent recipients of agonistic acts from both cows in general and mothers in particular (Fig. 13 and Table 20). The distance at which an approaching calf elicits an agonistic reaction is variable. It is usually under 10 feet and often as little as 5 feet. The variation in tolerance does not seem to depend upon whether or not the approached cow has her own calf present at her side.

Threat responses are not the only reactions shown by mothers at the approach of calves other than their own.

They may show avoidance responses (7 observations) or show no reaction at all (3 observations). In four of the first seven events the cows were approached simultaneously by two or more calves and were apparently unable to determine which one was their own. On these four occasions the cows ran from the calves.

Cows without calves that appeared to be non-breeding individuals (young, unantlered cows) most commonly showed an avoidance reaction to the approach of calves. The intensity of this reaction ranged from stepping away a yard or two to actually running away.

I recorded nine observations of cows unable to identify their own calf. In the resultant confusion of three of these events cows showed antagonism towards their own calves. Head bobbing and smelling of calves occurred in the majority of the other events. Often a mother smelled two or more calves and then directed a threat towards the strange calves or else simply attracted her own calf to follow. When a mother reacted to the presence of more than one calf by fleeing, her own calf was twice observed to continue to follow her after the others had given up.

Blauvelt (1955) notes that sheep usually smell more than one lamb and identify their own on the basis of comparison. Such smelling of two or more caribou calves was observed. Caribou cows concentrated on the anal region, along the back and around the muzzle when smelling calves.

Attempts by cows to attract calves away from their mothers were recorded seven times. In four of these events

the luring cow used head bobbing, and in the other three cases, attraction poses (see below) and grunting. On three additional occasions cows attempted to induce following in strange calves that were not with their mothers.

More often, however, calves left their mothers and started following another cow without any inducement from that cow. Occasionally calves followed another cow without her apparent knowledge. It is in this manner that two calves were able to make successful nursing attempts on strange cows. Most frequently the approach of a strange calf stimulated either a threat or avoidance reaction. Only once did a previously uninterested cow attempt to induce following after being approached by a calf.

Regardless of whether a calf was attracted away from its mother or left her on its own initiative, the mother usually intervened before any long series of interactions between the calf and another cow could take place. The mother's behavior was directed primarily towards regaining control over her calf. In four of the seven occasions when calves were lured away the mother reacted with brief agonistic behavior towards the other cow and then turned her attention to the calf, in the other three cases her activity was directed entirely towards her own offspring.

The attraction pose, most commonly appearing in the above type of situation, is held while the mother attempts to move between her calf and the other cow. The neck is held very low and bent convexly downward so that the head is at

the calf's level. The top of the cow's head is parallel with the ground (Fig. 18). This pose with the mother's head to the rear or to one side of the calf's body, as shown in Fig. 18, occurs when the mother is fleeing from a source of alarm or when she is attempting to induce her calf to cross a river or similar obstacle. When the cow uses the "attraction pose" to attract her calf away from another cow she either approaches from the side and holds her head beside the calf's head or she approaches the calf almost head-on. It appears that in such a position the mother is able to make maximum visual, auditory and olfactory contact with her calf.

Mothers show little tendency to move in defense of their offspring when these are not immediately beside them. On numerous occasions calves received threats and were chased by cows within view of their mothers, but on only two such occasions did a mother then move to threaten the other cow. It appears that a mother defends an area that is centered on herself and not the calf. Whenever separation occurs the efforts of the cow are directed towards inducing the calf to return to this defended area.

On two additional occasions I observed a cow-calf pair harried by a second cow that continually tried to place itself near the calf and attract it away from the cow it was following. In both cases threats and charges by the latter eventually discouraged these cows. Pruitt (1960) reports observing such associations several times and calls the second cows "assistant mothers".

There were many observations that demonstrated the ability of cows to recognize the bleating of their own offspring. Similarly, calves were seen to recognize the grunts of their own mothers (App. A, No. 7). For example, in a group of resting calves whose mothers were widely scattered, feeding, when one mother became nervous and started grunting only her own infant rose and ran to her. The other calves gave no reaction until their mothers also became disturbed.

When frightened a cow will give a few loud, hoarse grunts. Under normal conditions a long series of soft, intermittent grunts is given to elicit following by the calf. Under any type of disturbing conditions or when mothers and infants are becoming separated, such as while a nursery band moves through tall willows or makes a river crossing, both cows and calves will be continually grunting and bleating. During rain storms in late June and July calves are particularly noisy, presumably as a result of discomfort.

The Yearling in the Calving Group

Yearlings retained many calf traits, particularly during the calving and post-calving periods. They tended to follow cows closely and to adjust their activities to those of the cows. This tendency was observed most frequently in late May but also was shown as late as the first week of July. Smelling of cows by yearlings, or attempts to do so, and smelling of yearlings by cows was seen frequently although such interactions were rare among adults. Yearlings showed more curiosity than adults but were not likely to show an

escape reaction to a disturbing stimulus until the adults did so, even though they became aware of the stimulus first.

There is little evidence to indicate whether any yearlings on the calving grounds are still associated with their own mothers or whether they simply associate with other cows after being driven off by their mothers. In fact, it is still not clear to what extent they are actively driven off by their mothers. Further understanding of this topic will require observations of tagged animals. I have already shown however, that yearlings tend to occur in calving groups in about the same numbers as the unantlered (barren) cows in these groups. Many of these cows are themselves only 2 or 3 years old. An association between yearlings and unantlered cows was also indicated by observations of behavior. Unantlered cows appeared to show greater tolerance towards yearlings.

In both 1962 and 1963 the first cow seen with a newborn calf was harassed by yearlings. In 1962 the cow in question was continually approached by three yearlings. Her calf attempted to follow a yearling twice, and one yearling was nearly successful in suckling her. After several minutes of this harassment the cow left the group, moving off by herself. The yearlings did not follow. The mother of the first calf observed in 1963 was similarly bothered by two yearlings and eventually left the group with which she had been feeding. This cow was observed to remain wary of all other individuals for several hours, although she eventually joined another mother with a neonate calf.

On three occasions cows were observed to flee from yearlings attempting to follow them. One yearling chased a cow and her calf steadily for 20 minutes, the cow always maintaining a distance of 100 yards between herself and the yearling. Eventually the yearling gave up and moved off towards a small group of feeding caribou. By this time the calf of the fleeing cow was completely exhausted. These observations indicate that yearlings may be unstable and disruptive elements in calving groups.

Four observations were made of yearlings suckling, all in 1962. Three of these observations were made by myself, one by Kantner. Two of the events occurred after the end of the calving season, on June 30 and July 1. In none of the cases was the cow accompanied by a calf and in three cases the cows were unantlered. None of the cows appeared to be pregnant, although diagnosis of pregnancy on the basis of body-form has not been totally reliable. There is no way of knowing whether any of the yearlings were actually the offspring of the cows they nursed but in view of the harassing behavior of several yearlings directed towards one cow, as described above, it seems that this need not be the case.

In all four events the yearling adopted the side position with its rear towards the mother's head. In three cases the yearling kneeled while suckling. One single nursing event was all that was observed for each yearling, the duration of which ranged from 5 to 15 seconds, with the cow terminating. After two of the nursing events the yearlings were observed

to follow closely behind the cows until the animals were lost from sight.

Nursing by 12-month-old individuals is reported as a relatively normal occurrence in domestic reindeer herds (e.g. Jackson, 1897).

Social Facilitation

I have already mentioned that individuals within groups tend to show synchrony in their activities. In another sense, however, it might be said that individuals showing synchrony in their activities tend to form groups. Thus, as we have seen, after the peak of calving cows with calves tend to join together to form nursery bands.

De Vos (1960) described synchrony of activity in caribou bands and also noted that this synchrony tends to be greatest in small groups (under 50 head).

Within mixed groups cows with calves seemed most likely to establish the activity pattern, unless they formed a small minority of the individuals. Yearlings showed the most pronounced tendency to adjust their activity to that of others.

There were also many occasions in which one group reacted to the activity of another group. This inter-group facilitation often led to the union of two groups. For example, when a moving group passed close to a resting one, it might stop and join the latter, thus causing a mixing of the two. On the other hand, a more likely result was for some of the

resting individuals to move off with those passing by and some of the moving ones to stop and feed or lie down near those already down. Thus there was an interchange of individuals between the groups. Such an everyday event demonstrates both the importance of individual "mood" in social facilitation (see Crook, 1961) and the very temporary nature of the groupings.

When one group is running from some source of disturbance another group may react with similar escape behavior. This latter group may take a course parallel to, or diverging slightly from, that of the first. Thus social facilitation may occur without the following response that is so strong in intra-group reactions. Because of their greater sensitivity to visual stimuli cows with calves are most likely to react to the escape behavior of other groups.

During the crossing of rivers inter-group facilitation and the following response may be very pronounced and lead to the coalescing of groups. The following response is most evident in such situations during the late calving season and early postcalving period. The manner in which a few animals crossing a river may induce others to follow is best understood from a description of a specific event, one of eight similar events described in my notes.

June 22, 1961: Two groups, each approximately 500 head, move towards the Utukok River where they converge along the banks at 9:50 p.m. All are resting or feeding along the river, except a few moving slowly along the edge of the water. At 9:51 a dozen caribou begin to swim across.

Immediately all feeding individuals start to move towards the river and resting individuals nearest the crossing spot are looking up and rising. The wave of activity spread so rapidly that by 9:56 all the 1,000 animals have crossed the river or are in the process of doing so. Scattered individuals apart from this main mass are running towards the crossing spot from over a quarter-mile away.

Events such as this one are common and are important in the formation of large aggregations at the end of the calving season and in the establishment of a well-defined pathway of movement after calving. However, the process of coalescence occurs without any accompanying circumstances such as disturbance or river crossings. It appears most commonly that a small group will move towards convergence with a larger group. In June, 1962, during a period when only a few groups were visible at any one time, this process could be observed over the course of several hours as one group slowly moved towards another until the two were no longer distinguishable.

VII. THE POSTCALVING PERIOD

The Postcalving Aggregations

The period that starts when there is no further measurable increase in the proportion of cows with calves has been referred to as the postcalving period, although occasional newborn calves were seen in the postcalving period as late as July 3. The end of the postcalving period is not distinct but occurs as the large aggregations break up, usually in mid-July (Fig. 21). In 1961, however, a few loose aggregations of 5,000 to 10,000 were observed in the first week of August. The movements during this postcalving period are distinct from those beginning in late August in which the population begins to move towards the winter range.

The processes of change that begin in the late calving period continue into the postcalving period. Groups are constantly coalescing and the population becomes increasingly concentrated along one or two major pathways of movement (Fig. 7, p. 21). This process continues so rapidly that by the end of June more than 90 per cent of the population is concentrated in two or three masses (App. A, Nos. 15 and 16). The maximum size of these aggregations is maintained for only 2 or 3 days before the process of disintegration begins. It is not clear why this rapid reversal occurs, but many factors appear to play a role. Insect activity becomes increasingly distracting and annoying in early July. In addition, as the caribou obtain their thin, dark, summer pelage, they are not only more susceptible to insect annoyance, but

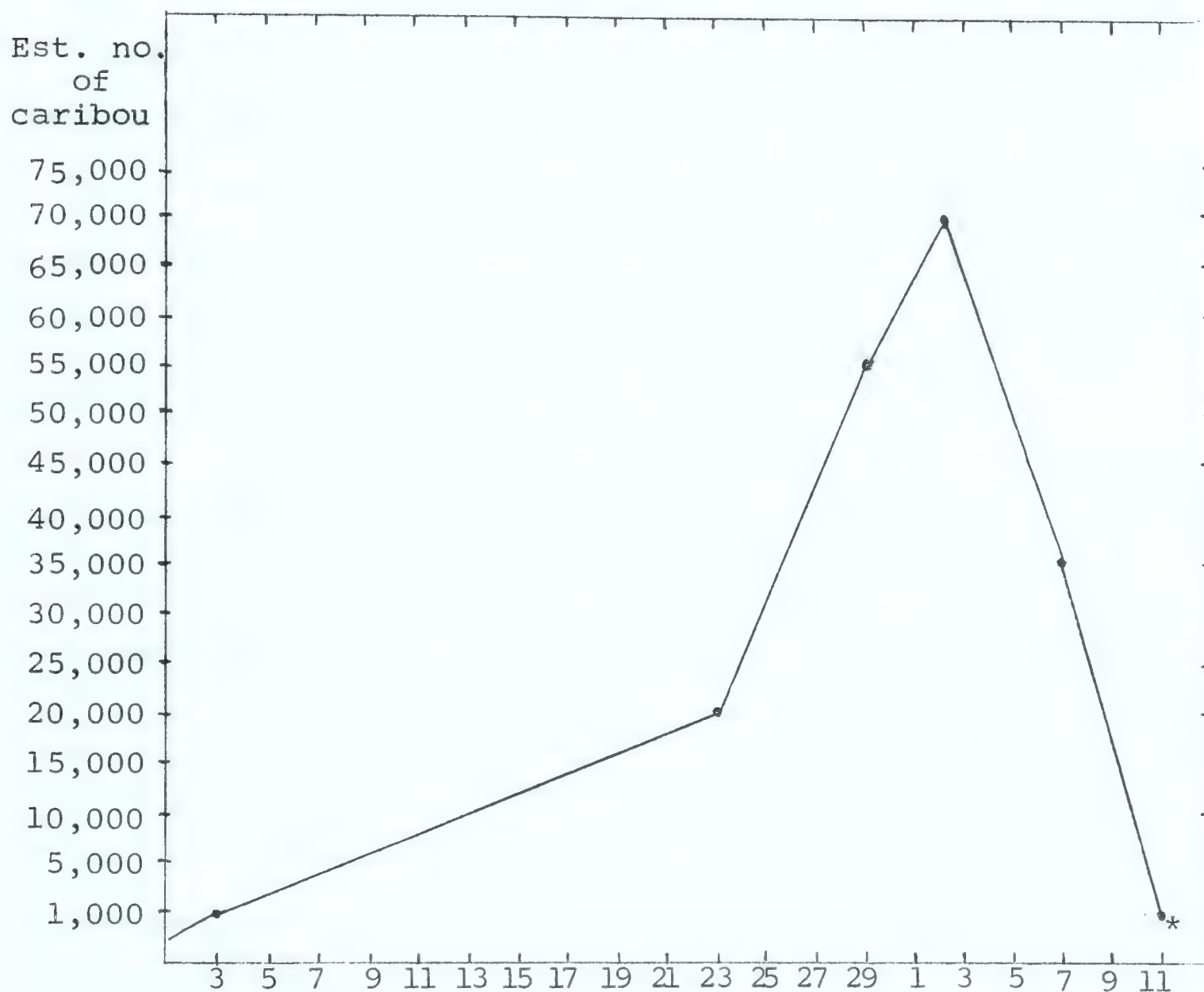


Fig. 21. Changes in maximum size of aggregations during late calving and postcalving periods, June 3 to July 11, 1961. (An aggregation appeared as one continuous mass of animals when viewed from the air).

* Slightly larger aggregations may still have existed in inaccessible mountainous areas.

they also are less conspicuous to one another. The general decrease in the sensitivity of the cows to social stimuli must also be of importance in the breakup of the population. Finally, the rugged, complex topography through which the caribou travel in early July may be a facilitory factor. The progress of specific groups was followed from the air in June and July, 1960. During late June the rate of travel of most groups was 10 to 20 miles per day and by mid-July some groups were observed to cover 30 miles in a day.

Several writers have remarked on the "tameness" of caribou when they are traveling in large aggregations. The statement is often made to the effect that caribou "feel safer in numbers" (Murie, 1935; Banfield, 1954; Kelsall, 1957). Harper (1955) suggests that the possibility of any one animal in such a large number being taken by a predator is very small, consequently no well developed fright responses have been produced. A discussion of seasonal changes in fright reactions appears in the following section.

Recombination of the Sexes

The changes in group composition that are underway late in the calving season continue during the postcalving season. Most striking is the increase in the proportion of adult males. This change, as it occurred in 1961, is shown in Table 21. The recombination of calving and non-calving segments of the population is the most important event of the postcalving period. In northwest Alaska, in all 3 years of my observation, the postcalving migration swung in a wide arc,

Table 21. The proportions of calving and postcalving groups composed by adult males, May to July, 1961.

Period of observation	Total no. of animals identified (including calves)	No. of adult males	Proportion adult males
May 28 - June 4	635	1	0.15%
June 5 - June 8	629	2	0.3 %
June 12 - June 20	9,178	59	0.6 %
June 22 - June 23	2,819	30	1.1 %
July 5 - July 10	3,073	959*	30.0 %

* 44% of adult individuals

moving first to the southwest, then back east, south of the calving grounds, and finally north on the east side of the calving grounds. Thus the calving segment passes through much of the area over which the mature males are distributed as a result of the precalving movement and their movements during the calving season. At the same time most of these scattered non-calving groups are moving towards the main concentration of animals. By early July the proportion of adult males is as high as, or higher than, that occurring in rutting groups. This complete mixing of the sexes is in contrast to the events described by Pruitt (1960:29), but similar to the findings of McEwen (1963).

Maternal Behavior

In these postcalving masses of several thousand caribou traveling 10 or 20 miles a day the possibilities for separation of cows from their calves are great, especially under conditions of confusion or stress, such as at river crossings or during attacks by predators. Such separations were actually observed as were the reunions of mothers and their infants (App. A, Nos. 16-20). In no case where the entire sequence of events was observed was the interval between separation and reunion more than about 2 hours. But there were other cases where one member of a reunited pair had been observed alone for most of one day.

Other observations indicated that separations may be permanent. Several deserted neonate calves, in apparently good condition, were found. Almost all of these were observed

at the end of the calving season or early in the postcalving period. In addition, in late June of 1961 aerial observations were made of a surprising number of lone calves, both dead and alive, along the pathways of migration. Two parties of oil geologists working on the Arctic Slope at this season also commented on the fact that stray young calves often appeared in their camps after the passage of large groups of caribou. The calves these parties had observed, as well as the majority of deserted calves seen by me, had certainly been born near or after the end of the calving season. It seems likely that the cows were stimulated to move off in the rapidly traveling aggregations before forming a sufficient attachment with their neonate calves. In the case of the latest newborn calf observed, the mother, although undisturbed, swam across a stream leaving her calf on the opposite bank and soon disappeared from sight.

In July and August, cows are still occasionally seen looking for separated calves. That is, the searching response has not entirely waned. For example, on August 7, 1960 I shot a calf from a hiding place so that I was not actually seen by the mother. The cow was frightened by the shot and moved away behind some willows at which time I removed the dead calf. She returned in a few minutes and searched for the calf then moved off with groups migrating through. Altogether, she returned three more times; the last observed occasion was 12 hours after the calf was killed. At this time she searched within 200 yards of the spot where

it had been shot, occasionally grunting softly. Banfield (1954) also describes a cow that in mid-August remained for 3 days at the site where her calf was killed by a wolf.

In spite of the urge to remain with the mass of the population, cows will reverse their direction of travel when separated from their infants. If one backtracks with an airplane in late June or early July along the trails left by the passage of several thousand caribou, a few lone cows are usually seen moving counter to the migration. In addition, lone cows, cow-calf pairs, and occasionally lone calves may be seen moving rapidly towards the main mass. Such lone calves are completely unwary and, in fact, may be attracted by any movement or sound.

By late September or early October searching behavior diminishes greatly. Cows were seen to stay in the vicinity of dead calves for only a few minutes and to leave without returning if greatly frightened.

Play by Older Calves and Other Individuals

Older calves occasionally sparred with their foreheads and spike-antlers or "boxed" with each other using their forefeet. Sparring among yearlings and 2-year-olds was seen more frequently than among calves but "boxing" was not observed. Extended chasing was rare among all age classes. On two occasions excitation leaps were observed in play. One of these occasions was the longest play sequence observed during this study (App. A, No. 10). This play lasted half an hour and involved a 5-month-old calf and a yearling.

Play among older animals occurred only under the stimulus of a hard snow or ice surface. When walking across a hard snow or ice surface, particularly when these were isolated patches surrounded by bare ground, young animals, and occasionally adults, were stimulated to perform bucking, frisking, twisting and other similar antics (Fig. 20). This behavior, as it occurs in elk, is shown beautifully in the Walt Disney film, "The Olympic Elk". The behavior in caribou was most likely to occur on warm days in spring or early summer.

The most striking example of this phenomenon I observed occurred on July 8, 1961, when large numbers of caribou were crossing aufeis on the upper Kugururok River. Almost every animal crossing the aufeis showed some unusual behavior. In the course of a few minutes the following events were observed: seven animals reared and struck at others, two cows butted others with their foreheads, two pairs of males met head-on and a yearling charged a cow and struck her in the side. In addition, yearlings, adult males and once an adult female attempted to mount other individuals. Of greatest interest was the fact that all the males, including the yearlings, had their penes extended while crossing the ice.

It is possible that the cooling effect of the large expanse of ice in some way provided the stimulus for this behavior. However, on other equally warm days animals were seen crossing and resting on ice surfaces without any similar behavior.

VIII. DISCUSSION

Behavior Associated with Parturition

The question arises of whether cows actively avoid other caribou before the time for parturition. Pruitt (1960: 26) suggested that they do, when he wrote, "I gained the impression that females dropping their fawns either early or late tend to separate themselves from other caribou. Those dropping their fawns during the peak of fawning form 'maternity bands' ..."

I consider such behavior to be the exception rather than the rule, regardless of the stage of the calving season. As I have already described, cows giving birth are more often merely left behind by the groups they are with. This is more likely to occur early or late in the calving season. "Maternity bands" form at the peak of calving only because a large proportion of the cows are giving birth at that time. The cows that gave birth earlier tend to aggregate together and travel at a slower speed. De Vos (1960) also observed that cows show no particular activity before parturition but that after the birth they move off in the direction of the bands they had been with.

The observations summarized in Table 11 are also at variance concerning the cow's position at the time of delivery. Pruitt, Kelsall, and Wilks all observed parturition to occur in the reclining position. The cows I saw in normal parturition were all standing as was the cow during the still-birth I observed. In feral reindeer, Curry-Lindahl, Nordiska

Museet, Stockholm, (pers. comm., 1963) reports that the standing position is common, but births in the lying position also occur. He notes, as I have also observed, that the cow may frequently change position during labor. J. Grimmer (pers. comm., 1963) reports that most of the reindeer which have given birth in the National Zoological Park, Washington, D.C., have completed parturition from a squatting position, so that the calf was dropped from about one foot above the ground.

Hediger (1955) states that cervids usually give birth lying down, and Naaktgeboren and Vandendriessche (1962) feel that this is the general rule for ruminants. But Slijper (1960) lists many ungulate species, including reindeer, among several other cervids, which may as a rule be standing at the time of delivery. It appears that the position of the cow during delivery is variable within the species. Such variability among the members of one species is common among ungulates as shown by the comparative data presented by Slijper (1960) and Naaktgeboren and Vandendriessche (1962).

The duration of labor is also highly variable in many species (see Slijper, 1960; Naaktgeboren, 1963) including the caribou (see Table 11). On the basis of the few observations compiled, 30 minutes appears to be a typical duration of labor in the caribou and in this it does not differ appreciably from other cervids.

Slijper (1960) and Naaktgeboren and Vandendriessche (1962) both believe there is good evidence that mammals usually give birth during the normal resting hours of their species.

Both Harper (1955) and de Vos (1960) consider the hours around mid-day to be a time of decreased activity for caribou. However, I have shown that, although I observed a greater frequency of births during the mid-day hours, this difference was not significant. In addition, McEwen (1960) observed only one out of seven births during these hours. In view of the uncertainty of the observations, more data are certainly needed on the subject.

I observed the placenta expelled from cows in the standing position in several instances, although Pruitt (1960) implies that it normally occurs in the lying position. The time between birth and the expulsion of the placenta was again quite variable, ranging from a few minutes to 2 hours or more (Table 11). Slijper (1960) comments that such individual variability is the case in many species.

All the caribou cows observed by me and the other workers cited in Table 11 commenced licking their calves soon after giving birth. Many functions have been suggested for this licking activity on the part of ungulate mothers. In the discussion appearing in Blauvelt (1954) among those mentioned are stimulation of respiration, removal of fecal plugs, improvement of muscle tone, establishment of the nursing position, and establishment of the mother-infant bond.

Brownlee (1957) believes that licking plays an important role in establishment of the mother-infant bond in domestic cattle. However Collias (1956, and in Blauvelt, 1954) points out that in goats great variability in the

licking behavior of mothers is evident and does are known to have accepted their young without ever having licked them.

In addition to the functions suggested above, licking must be important as a means of drying the calf's hair. The insulative qualities of a wet calf's skin have been demonstrated to be far inferior to those of the dry skin (Hart et al., 1961). Thus the licking of the calf must be of great survival value during times of severe weather conditions.

The importance of the drying effect of licking in ungulates is also suggested by Naaktgeboren and Vandendriessche (1962) who note that in the camel and dromedary the fetus has an unusually well developed epitrichium and the neonate is never licked. The epitrichium is broken during the expulsion and first movements of the fetus.

The frequent contact which the caribou mother maintains with her infant during its first days of life and her efforts to induce her infant to follow her away from the place of birth are in contrast to the behavior shown by many forest-dwelling deer in which the young remain near the place of birth, perhaps for several days, while the mothers forage at some distance from them. Severinghaus and Cheatum (1956) state that white-tailed deer are left shortly after birth and only visited every 2 to 3 hours for nursing. Darling (1937) states that red deer calves are visited only twice a day, but unfortunately he gives no indication of how soon after birth such a schedule commences. Most interesting

is the information given by Perry (1952) suggesting changes in the maternal care of red deer. Under the present conditions in the Scottish Highlands the red deer are primarily inhabitants of the uplands and the low heather of the afforested areas. This distribution contrasts with their former use of forested and high heather habitats. The "mountain babies", as Perry calls the calves born in the barren uplands, appear to receive closer, more frequent attention than the "glen calves".

It is likely that a similar modification of maternal behavior has occurred on a broader scale among the cervids and within the genus Rangifer, also. Unfortunately, I know of no observations of maternal behavior in the woodland caribou with which a comparison could be made to that of the barren-ground caribou. The only published mention of the topic is that of Dugmore (1913:18), a keen observer and wildlife photographer, who wrote:

How soon the mother leads her little one out of the shelter of the forest I do not know, probably not for several days, for outside the woods the flies are worse even than among the trees; she guards her offspring with the tenderest care, seldom leaving it for any length of time, always affectionate and solicitous for its welfare.

From what little is known of the origin of the genus Rangifer (see Banfield, 1962), we might expect that the adoption of the forest-dwelling habit came later after the spread of the

genus in late Pleistocene times.

Maternal behavior patterns that overrule the usual gregariousness and responsiveness to social facilitation of the barren-ground caribou cow must develop almost immediately after birth, if the calf is not to be deserted. In other words, some immediate stimuli must be provided to keep the mother at the place of birth. The observations of behavior following stillbirths indicate that these stimuli are provided by the living neonate and only to a much lesser extent by a dead calf or by any physiological effects of parturition itself. What stimuli are most important cannot be ascertained on the basis of the purely observational data. It appears that all modes of sensory reception play a role.

However the frequent cow-calf contacts act to strengthen the cow-calf bond, there is no doubt that in caribou the bond is at first unidirectional and is only maintained by the persistent efforts of the cow. The manner in which the young calf may abandon its mother and attempt to associate with other individuals has already been described.

Although the cow-calf bond starts to develop almost immediately it does not reach maximum strength for the cow for at least some hours and for the calf, not for days. I have described how desertion was most prevalent among cows giving birth near the end of the calving season when group responses and the urge to migrate have their strongest influence on the cows.

Head Bobbing

In his discussion of head bobbing Pruitt states that the act occurs in situations having apparently different motivations and that the movements might be "... derived from still another movement of perhaps one from the others" (1960: 11). I have shown (p. 85) that the majority of these situations are ones in which the animal performing the head bob is presented with a conflict of drives. It was also observed that the head bobbing movement most closely resembles the neck movements of a feeding caribou.

Grazing caribou are constantly moving and executing feeding movements during short pauses. With a pattern of feeding activity such as this, individuals are often disturbed in the course of a feeding movement, thus the head is dropped almost to the vegetation but is brought up very quickly to the alert position. When an individual is in motion it always pauses briefly when head bobbing, just as with the feeding motion. The likelihood of head bobbing occurring when feeding animals are presented with a conflict situation is probably increased by postural facilitation (see Tinbergen, 1952:18) but the same motion occurs in conflict situations (Table 16) where no actual feeding behavior is involved.

Recent papers (Van Iersal and Bol, 1958; Sevenster, 1961) have stressed the importance of a conflict of drives in the causation of displacement activities. Their hypothesis of disinhibition appears to offer an explanation for almost

all observed cases of head bobbing. According to these workers, in events where the disinhibition (conflict) period is brief, the displacement activity is more often incomplete. Such is the case with most head bobs occurring in alarm situations.

Earlier I described how the head bobbing act performed by cows towards their calves induces the calf to rise and approach or follow her. Thus the act serves as a social signal or "releaser" under these circumstances. As a displacement activity having obtained releaser functions, head bobbing meets most of the criteria usually associated with ritualized acts (as discussed in Blest, 1961). It is difficult to say to what degree the act has become emancipated from its original causal factors and the concepts of such emancipation and its neurophysiological implications are not at all well defined in the literature. Under certain circumstances, as when a cow attempts to attract its own calf but is not itself attempting to travel, there is no overt conflict apparent in the situation. In such cases the act might be said to be fully emancipated. Van Iersal and Bol (1958) have rejected the distinction between autochthonous and allochthonous causation and refer instead to "facilitation" by "+ factors" of a specific displacement activity. As is described in Section 6, head bobbing does not always occur in attempts by mothers or other cows to elicit following. Other signals have equal valence for calves. Whether this means that certain facilitory "+ factors" are lacking when

head bobbing is replaced by other signals is unclear.

Head bobbing by a cow towards her calf presents the calf with a repetitive stimulus in which the form of the head is moved rapidly across the plane of the calf's vision and appears in contrast to the background. In these qualities head bobbing is similar to experimentally produced stimuli known to induce or strengthen approach and following responses in birds (see Smith 1960, 1962; Fabricius, 1962).

Social Control of Agonistic Behavior

I have previously noted the low frequency of actual animal-animal contacts in agonistic interactions (Table 19). Actual striking of calves was observed only three times, or in about 6 per cent of the cases in which agonistic acts were directed towards them. It is doubtful if any of these blows from the forelegs of cows were enough to cause serious injury. Calves appear particularly adept at avoiding agonistic acts.

Other workers, however, have reported calf mortality apparently resulting from cow aggression. Skoog (1956), Kelsall (1960) and de Vos (1960) report the finding of a few dead calves with puncture wounds and bruises.

Although under certain conditions calf mortality may result from agonistic interactions, it must be considered relatively rare. Most agonistic activity clearly results in no contact between individuals.

Not only is there little contact, there are no long sequences of agonistic behavior, at least outside of the

rutting period. There were only 5 agonistic events out of 134 in which the recipient of a threat reacted in turn with a threat. In one of these 5 cases the original threat was reinforced with a second threat and the recipient moved away. In the other 4 cases the original threatener retreated when it received a threat in return. Besides the 3 head-to-head contacts and 2 rearing contacts (Table 19) there were also 5 non-contact events in which both participants acted simultaneously.

The picture presented by all my observations outside of the rutting period is one of a gregarious species in which almost all agonistic interactions are brief, involve no physical contact, no group disturbance or participation, and no injury to the individuals involved. Threat is usually unidirectional, with the most frequent reaction to it being simply one of avoidance. Intense escape reactions are not seen, nor are there any conspicuous submissive postures. Groups are completely open, individuals joining them are never met with any overt hostility nor is any seen when groups meet and intermingle. This description does not apply fully to rutting groups but in these, too, the groups are relatively open and tolerance is high towards males that are not actually engaged in courtship and mating activities at any given time.

An organization of agonistic behavior such as this cannot be fitted into any of the existing schemes for the classification of social hierarchies or social groupings (such as that proposed by Collias, 1944). In spite of many

reviews of the topic of social controls of aggression, the subject is still confused. Because of the preponderance of experimental work with domestic animals and small groups of animals in confined conditions it seems that undue emphasis has been placed on the role of individual recognition in the formation of dominance hierarchies. Scott (1958:173) has clearly pointed out that "dominance relationships in captivity can be strengthened or even created where none existed before." Although he suggests only that this can be due to an unnatural concentration of food supply, it is likely that in some instances unnatural dominance relationships can be established merely by an opportunity to recognize other individuals that might never occur under natural conditions. Barren-ground caribou clearly have no opportunity to learn to recognize the individuals with which they interact. Schneirla (1946) also criticizes the overemphasis on dominance hierarchies, particularly those that may become apparent only under rather special conditions.

In his recent treatment of this topic, Wynne-Edwards (1962) places emphasis on the importance of individual recognition in the formation of dominance hierarchies. He states (p. 137) "... it seems probable that the size of social units is often partly determined by the consequent need for individual acquaintance and the limitations imposed by a finite ability to remember 'faces', as it were." Whether the above ability is actually a "need" or whether other limitations are in reality acting has yet to be investigated in any wild popu-

lation, to my knowledge. Wynne-Edwards goes on to state that where the number of individuals is large "... individual meeting and acquaintance are out of the question and establishing a detailed hierarchy therefore impracticable."

In these cases, Wynne-Edwards suggests that competitive striving in epideictic displays is substituted. He believes (p.413) "... prairie-like country greatly enhances the visible epideictic effectiveness of animals in herds roaming together over their common feeding grounds."

I am uncertain how this epideictic display might operate in caribou or how it could result in feedback that would stabilize population levels, as Wynne-Edwards suggests it does for many species. Possibly some such mechanism might be responsible for the increased length of migrations that have been observed concurrently with the increase in size of certain caribou populations (see Section 5).

Collias (1944), in his tentative classification of vertebrate social groups, implies importance to individual recognition in his emphasis on "closed groups" as opposed to "open groups". He considers frequent fighting to be one of the attributes of open groups and that greater tolerance is concomitant with groups that are "more evident and coherent" (p. 90). He further feels that the social order is most stable in groups which cooperate as units in competition with other social groups. Although there is good evidence that these are widely applicable rules, caribou provide an exception. The caribou group is temporary, completely open, and does not

act as a unit in competition with other groups. In spite of this, fighting is infrequent and tolerance very high. It appears likely that such open, high-tolerance groups occur among other ungulate species as well.

The work of Reynolds (1963, 1964) clearly shows similar open groupings with high tolerance in a primate, the chimpanzee (Pan troglodytes shweinfurthii) of East Africa. Reynolds suggests that such a loose social structure permits convergence on temporary concentrations of food, thus achieving a more efficient exploitation of food resources. This behavior seems analogous to that of the caribou and of many ungulates inhabiting arid or semi-arid areas. Thus an additional category to include such groupings is necessary in Collias' scheme. In his discussion of this topic, Thompson (1958) does point out that high group stability is not necessarily associated with low aggressiveness. However, he also emphasizes the importance of individual recognition and territorial behavior in controlling aggressiveness.

Unfortunately there are no quantitative data from other studies by which a comparison of the frequency of aggressive acts and the ratio of "threat-only" to "physical-contact" events might be made. Such a ratio might serve as a useful indicator of differences between species in intra-group tolerance as well as being an indicator of the degree of social stress any group is subject to under different conditions. Even the detailed study of social dominance in cattle by Schein and Fohrman (1955) gives no information on

the relative frequency of these two types of events, although the authors note the occurrence of both types.

The question may be asked then, if caribou do not establish dominance hierarchies on the basis of individual recognition, how do they maintain social order and avoid frequent conflict in open groups? It appears that the best approach to understanding the methods of organizing agonistic behavior lies in comparing the ontogeny of social behavior in different species. Scott (1962a) points out that three methods exist for controlling social fighting: 1) systems of territorial organization, 2) organization of social-dominance hierarchies in which a regular relationship of threat and avoidance develops through learning and habit formation, and 3) social controls arising in connection with primary socialization.

The first of these methods is of no importance in barren-ground caribou, although it might play a role in non-migratory populations. Methods "2" and "3" above are not easily separable. Allee (1952:158) uses the term "social-hierarchy" in the broadest sense to mean any social rank-order established through direct combat, threat, passive submission, or some combination of these behavior patterns. He includes under this definition such simple types of dominance as that between dogfish (Mustelus canis) in which dominance appears to depend entirely upon the relative size of the two interacting individuals.

To digress for a moment, it appears that the patterns

of "mutual evasion" performed by dogfish, as described by Allee and Dickinson (1954), show a great similarity to the epideictic displays described by Wynne-Edwards (1962) in many birds and fish, as well as invertebrates. The possibility of patterns intermediate between epideictic displays and true dominance-subordination interactions should not be overlooked in consideration of the evolution of dominance-subordination behavior.

Obviously some distinction should be made between the simple type of dominance shown in the dogfish and that involving individual recognition of other individuals, or even awareness of the changes in relationships between other individuals in groups as, for example, in the rise in dominance of female birds mating with alpha males (Lorenz, 1952).

A new classification system should recognize the differences between dominance hierarchies based on directed social releasers and hierarchies in which these releasers are not used, as well as the differences between hierarchies based primarily on recognition of individuals and those based simply on recognition of classes of individuals or on the recognition of certain acts (social releasers) performed by those classes.

The dominance hierarchy in caribou must be based primarily on the recognition of classes of other individuals or the social releasers presented by these classes, and, within classes, on various conditions occurring at each individual encounter. The hierarchy of classes as it occurs

in caribou during the calving season is shown in Fig. 22. Between the different classes the dominance is almost purely a unidirectional one (a "peck-right" hierarchy).

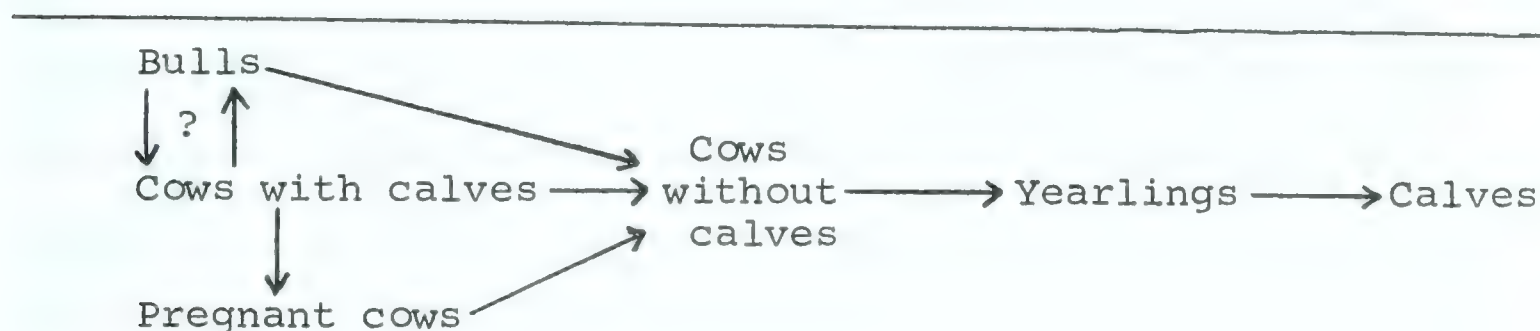


Fig. 22. Class dominance hierarchy at calving time.

Of the five cases noted above in which the recipient of a threat reciprocated with a threat of its own, three of these occurred within classes, the other two were directed by cows without calves towards cows with calves, indicating that "mistakes" might have been made in which a cow did not recognize the fact that another cow was accompanied by a calf. In both these latter two cases the cows without calves immediately withdrew when threatened. No agonistic interactions were observed within the yearling class during the calving season. Such interactions are rare until they start rutting activity in their second year, that is, at the age of 15 months.

It is only by examining the primary socialization of the caribou calf that we can gain some idea of how the agonistic behavior has become so organized.

In spite of the strong following response to moving

objects shown by the neonate, even the youngest calf will react with some attempt at avoidance behavior when presented with one of the threat poses. Whether these responses are due to some "innate releasing mechanism" or whether they result from reception of stimuli of unusual magnitude (see Schneirla, 1959 and discussion later in this section) is uncertain. The fact remains, however, that as soon as the calf has obtained the necessary motor ability it ventures forth and makes frequent contacts with other individuals. The "typical" calf in a nursery band is most likely to encounter a pregnant cow or a mother, from which it usually receives threats. It reacts to these with avoidance and often by withdrawal to the mother, thus the mother-infant bond is reinforced. Since some agonistic acts are potentially injurious to the young calf, selection operates in favor of rapid responses to threats. The infant is not protected from other classes of individuals by its mother to the extent occurring in other cervid species such as the moose (Altmann, 1958) or red deer (Darling, 1937; Eygenraam, 1963).

The caribou infant has no siblings with which it can engage in play-fighting and experiences no competition for the milk supply of its mother. It thus has no experience during its infancy on which a role of dominance or subordination within its age class might be formed and carried over into adulthood, nor would any advantage accrue to it by achieving dominance over other individuals in its age class before entering adulthood. There are no calf groups or periods of competitive play such as occur among other cervids

(Darling, 1937; Altmann, 1960). The infrequent infant-infant interactions are characterized by great uncertainty on the part of both participants (recall the frequency of head-bobbing). The brief encounters almost always end with the withdrawal of one or both calves to their mothers. Only five calf-calf interactions involving agonistic acts were observed. These encounters with other calves, as well as those made with older age animals, help the young calf to learn of the existence of other classes of individuals in its society. Thus they function in a manner similar to play in other species, including man, to aid in role-learning and in the learning of the existence of roles (see Bateson, 1955).

Thus from the nature of the infant's experiences during primary socialization a pattern is established that carries through into later life. The non-aggressive temperament that develops is modified markedly only by the changes associated with maternity and rutting.

Seasonal Changes in Fright Reactions

The sensitivity of caribou in reacting to stimuli shows great seasonal variation. Observers, such as those cited in the previous section, who have viewed caribou in the summer and autumn months have almost universally commented on the "tameness" of caribou. Kelsall (1957), however, speaks of bands becoming warier in August and the first part of September. Harper (1955:83), describing his experiences with caribou in the summer and autumn, is most emphatic regarding their lack of wariness and says that the caribou reacted

"... with little more concern than so many barnyard cattle." When he compares the caribou he observed with those described by Stefansson and other Arctic explorers he concludes that the caribou of the MacKenzie District and the Arctic Coast must be of a far wilder nature. Such a conclusion is not justified. I have observed just as much variation in wariness within the population of northwest Alaska, depending upon the season, weather conditions and other factors. The greatest change is apparent in the cows, which go from maximum wariness at the time of parturition to minimal wariness by mid-summer. As will be described below, these changes are most noticeable in reactions to visual and auditory stimuli and not as great in reactions to olfactory stimuli.

I have already pointed out that caribou traveling in the footsteps of others always tend to be less alert. This fact holds true even for small groups following along the trails left by the recent passage of a larger aggregation.

There are some interesting possibilities to be considered regarding the changes in responses of individuals in the large postcalving aggregations. First of all, the greatest change is associated with visual stimuli. Changes in responses to scents are erratic and not so clearly marked.

When a caribou views some suspicious object it may stop and give the alarm pose, but does not usually immediately take flight. (See de Vos, 1960, for a discussion of differences between the "alerting" and "flushing" distances). This delay between alerting and flushing is a common phenomenon at

all times of the year. If the alarm stimulus is not too great and if other animals do not react to it, or to the alarm pose of the viewer, that individual may never show escape behavior. The caribou may return to normal, or almost normal, behavior but often remains more alert than usual for some minutes afterwards.

When a mass of several hundred or several thousand caribou are moving together only a very few are likely to notice a visual source of alarm at any one time. The vast majority are either blocked from view of the alarm source by their fellows, or they are simply concentrating their gaze on a narrow field of view in front of them and never become aware of the alarm source. If one individual shows an alarm pose or starts to flee, it has little effect on the mass of others around it. Little attention is paid to the rapid movement of one or even a few individuals. When the disturbed individual sees that others are not alarmed it will normally discontinue its escape behavior. In aggregations of thousands, even a hundred or more individuals may become frightened but they meet both a physical and psychological barrier in the form of the caribou around them and they rapidly mix with relatively unalarmed individuals. Thus, again, there is a "dampening effect".

A different situation may arise with regard to alarming olfactory stimuli. In this case a great proportion of the individuals, even in a large aggregation, may receive the alarming stimulus simultaneously. Thus fright reactions

can easily spread throughout an entire group.

An example of this type of reaction took place on July 7, 1960, when 60,000 to 70,000 animals passed my camp in one day. These masses were extremely insensitive to fright by visual stimulus. I experienced no difficulty in approaching them within 50 yards, walking in the open. However, when I climbed a small knoll, a quarter of a mile away, so that a moderate breeze was blowing from me to the caribou, I was able to induce fright and running in about 2,000 animals. Under different conditions only some animals out of a large group may receive an alarming odor and then the same "dampening effect" would operate as with visual stimuli. In general, however, I did not note the decrease in reactivity to odors among large groups that Kelsall (1957) reports. Banfield (1954) describes how his scent affected a group of several thousand caribou, leaving a mile-long corridor downwind from him free of caribou.

A further factor that may influence fright reactions in such large migrating groups is a decline in responses due to repetitive stimulation. The individual caribou is constantly seeing movement around him by the thousands of individuals migrating with him. The repetition of this stimulus would result in increased filtering of such signals (see Broadbent, 1961, for a discussion of "filtering"). Such a response inhibition would not affect responses to stimuli via other sensory modes.

The importance of such filtering is indicated by

the results of a simple experiment carried out on occasions when large groups were migrating by me. I walked along a pathway parallel to a single file of caribou, 50 to 100 yards to one side of them and downwind. Under such conditions, I was usually able to walk in the same direction as the migrating individuals, and pass them by, without causing any alarm. Or, if I walked slowly, the animals would pass by me and continue on their parallel trail. However, when I attempted to walk on a parallel trail in the direction opposite to the movement of the caribou, I immediately attracted attention (from the unusual stimulus of movement in the opposite direction) and always caused alarm. When a cow that has been separated from her calf moves counter to the direction of migration searching for her calf, she will often similarly attract the attention of other individuals, who stop and stare at her.

The plague of insects is another factor that influences the summer reactivity of caribou. Kelsall (1957) noted that caribou are most easily approached during the height of the fly season. My own observations are in agreement that insects tend to distract and tire caribou to the point where they may pay little attention to stimuli that are normally alarming (App. B, No. 23).

Although caribou may react to perfectly still forms (such as a man seated quietly), they will usually show only slight avoidance responses or else investigate the object further until the odor is detected. The additional stimulus of strange odor or of movement is necessary to produce a full

escape response. The sensitivity of reactions to still forms varies but in general it can certainly be said that the perception of form and surface qualities must be very poor.

One example of the many experiences that illustrated this occurred in October, 1961. I was able to "imitate" a spruce tree by standing rigidly still in a clearing scattered with small trees, the nearest of which was several yards from me. Many animals filed by me, often within 15 feet. Occasionally individuals became suspicious and veered away to about 25 or 30 feet. Two calves stopped to "box" with each other only 10 feet from me.

The apparent inability of caribou to distinguish forms very well has been exploited in caribou hunting. The use of crude dummies was formerly widespread among caribou hunting cultures. Among other writers, Stefansson (1921) and Spencer (1959) describe the use of "inuksuit" ("likenesses of man") in a 'V-shaped' formation, often several miles long, to herd caribou towards a specific spot where hunters waited. Manker and Vorren (1953) describe a similar arrangement previously used in Norway to funnel herds of wild reindeer towards covered pits. Stefansson (1921) notes that some frightening stimulus was necessary to induce the caribou to start down the trap. People were stationed at intervals of approximately every half-mile along the lines of inuksuit to reinforce the frightened state of the caribou with noise and motion. Piles of stone only a foot or two off the ground

apparently produced an avoidance reaction equal to that of man-sized objects.

During the winter the caribou seem to be more sensitive to movements. This may in part be a compensatory mechanism for a decrease in the ability to detect odors under cold conditions.

Stefansson (1921) stated that a caribou in winter is able to detect a man visually at 400 to 500 yards, presumably this is with some degree of movement on the part of the man. He eloquently described the difficulties of winter hunting of caribou in an account of his experiences in Isachsen Land, where the caribou were not normally subjected to hunting by either Eskimos or whites.

Within the broad pattern of seasonal changes, weather conditions also exert a considerable influence on the reactions of caribou. Such changes in "irritability" have been well demonstrated in red deer by Darling (1937). By taking records of relative humidity Darling found that "irritability" was greatest at times of high humidity and particularly when the humidity was rising or oscillating. He emphasizes the importance of the olfactory sense in these irritability changes. Darling cites a statement by Klemola (1929) that great care is necessary with corraled reindeer at times of thaw, so as not to cause stampeding. Freuchen and Salomonsen (1958:101) note: "In early spring when the gales spring up suddenly without warning from every direction, the reindeer lose all trust in dog and man".

I have observed great changes in flight distance and especially in the differences between the alerting distance and the flight (flushing) distance, apparently associated with weather changes. Unfortunately there was no opportunity to record relative humidities. I will describe only one example of these observations here. On May 26 and 27, 1962, the temperature hovered around the freezing point with gusty winds and snow squalls. I approached several groups, walking towards them slowly from directly downwind. All groups noticed me and immediately ran off when I was between 250 and 500 yards away. On May 29 the air temperature was lower, but there were clear skies and warm sunshine with less wind. Under these conditions, on the same terrain and with groups of about the same composition, the caribou never fled until I was within 200 yards and I once approached a group to within 100 yards. The groups permitting the closer approach also did not flee as far after taking fright.

The caribou's reactions to noises are also variable. Stefansson (1944) described how it is possible to shoot an entire band of caribou without any fleeing from the noise of the rifle. According to Stefansson only the whine of the bullet or the noise of its impact will frighten a band. Murie (1935) noted how oblivious caribou may be to shouting and other noises. De Vos (1960) observed only mild alarm in groups hearing gunshots about one-half mile distant. However, I have seen groups in late June and early July that ran for several hundred yards when hearing gunshots at a similar distance.

Lone caribou are more easily frightened by noises. Also, I have gotten the impression that groups are more easily frightened by sounds when their visibility is limited, as in brush along river channels or even in small valleys or hollows. Just as Dugmore (1913) reported, I have had caribou take fright at the click of my camera and also from the "whirr" of my movie camera.

The greatest sensitivity to sounds occurs in winter, on calm days when the temperature drops below -20°C . Under such conditions I have had no difficulty hearing caribou digging feeding craters in the snow at a distance of 400 to 500 yards. They, in turn, appeared to hear and react to sounds I made walking on a crusted snow surface half a mile away. During 3 days of such conditions in February, 1961, caribou groups, particularly pairs, were often seen running across the tundra for no obvious reason. The only explanation I could offer for this behavior, was that they were being frightened by the noises of other caribou.

It has occurred to me that under such conditions the clicking noise produced by the sesmoid bones of caribou (see Jacobi, 1931) might permit caribou to identify approaching but unseen animals as either "caribou" or "non-caribou". However, I was never able to hear the clicking noise until the caribou were very close, long after I could hear the noise of their hooves on the snow surface.

The Behavior of the Infant Caribou: Some Theoretical Aspects.

I will here review some observations on the behavior of the caribou calf in its first days and consider how these events may be interpreted in the light of current concepts for dealing with the ontogeny of vertebrate behavior.

It is clear from the observations described at several points in this work that the rate of early maturation may vary greatly between individual caribou calves. Such variability greatly influences their early behavioral processes. Because of the extreme speed with which the neonate passes through phases of its ontogeny, variation of only 2 or 3 hours is relatively as great as a difference of a week or more in the behavioral development of puppies or human infants as described by Scott (1962b). Because of the rapidity with which development takes place and because there were only limited possibilities for experimentally manipulating the environment of the infant caribou, it is not at present possible to apply the "critical periods" concepts of Scott (1962b) to caribou. It was observed that the process of socialization begins immediately after birth (Table 11, see also discussion by Schneirla, 1963). The first half-hour or so after birth is certainly a "critical period" with regard to the identification of the cow with her calf. There was no indication, however, that removal of the calf from its normal post-natal social environment for up to a few hours prevented the normal release of social responses after its reunion with the mother.

When the neonate caribou calf first attempts to stand it orientates towards its mother and immediately after rising moves towards the mother until it makes contact with her or falls down. After contact, searching for the udder takes place. Essentially, this is the repertoire of behavior during the first hour. If unusual circumstances ensue so that the neonate is brought into close association with another caribou, or a human, approach movements occur until contact is made. No motions of searching for the udder occurred when calves made contact with humans. If disturbed by very rapid, pronounced motion or loud noises at close proximity the calf may withdraw by merely lying down.

Schneirla (1959) has discussed the importance of such biphasic phenomena in animal behavior and in particular with regard to theories of motivation. He contrasts the acts of "approach" and "withdrawal" with "seeking" and "avoidance", the latter two being of a higher evolutionary and developmental order. Schneirla considers that "approach" or "withdrawal" decisions are influenced only by the stimulus intensity and that all organisms pass through a stage at least in their early development in which only the simpler "approach-withdrawal" responses occur. He believes that, in general, approach is made towards low-intensity stimuli and withdrawal away from high-intensity stimuli. It seems more correct to state that organisms approach an optimum level of stimulation, which, while it may often be the lower of two intensity levels under normal conditions, is not necessarily so.

Baerends (1950) cites examples of work in which the importance of an optimal stimulus intensity has been demonstrated but even more pertinent are the theoretical concepts developed by Leuba (1955). He states: (p. 29): "The organism tends to acquire those reactions which, when over-all stimulation is low, are accompanied by increasing stimulation; and when over-all stimulation is high, those which are accompanied by decreasing stimulation". Leuba thus places emphasis on relative levels of total stimulation in facilitating learning processes.

The original response of the caribou calf is made towards a relatively low intensity stimulus: the mother's form. This, however, increases its total level of stimulation. Its positive response is reinforced by contact and by the licking and grunting of the cow, and presumably also by her odor. By thus raising their stimulation levels via several modes it is probable that learning processes in both the cow and the calf are facilitated.

Several experimental workers dealing with following responses and imprinting have also noted that imprinting occurs more rapidly and more strongly when the subject is exposed to distress-producing stimuli such as loud noises or mild shocks (see Hess, 1959, also studies cited by Scott, 1962b). However, when fear is too strongly developed the imprinting becomes weaker (Salzen, 1962). Leuba's theory that rapid learning is facilitated by mild tension-producing situations conforms with these observations. In a precocial

mammal the phase in which responses are purely stimulus-intensity dependent is passed through very rapidly. The neonate calf soon begins to seek and discriminate. In almost all cases the location of the udder is learned immediately and before its first four hours are ended the calf is able to move directly to the udder from different angles.

When the cow moves away from her neonate calf the approach response becomes, in fact, a following response, and the calf soon maintains a short interval between itself and its mother, without continuously attempting to make contact and nurse. Although this strong following response occurs there is no evidence that imprinting takes place at the same time (see below). The following response of the calf is reinforced by the low grunting of the cow and most strongly by her head bobbing. The effectiveness of head bobbing, at least at first, may also be based on an increase in the level of stimulation. I have already mentioned the similarities between head bobbing and the stimuli producing approach responses in young birds.

It is possible that other early behavior patterns of the calf are simply responses to different intensities of stimuli. I have previously discussed the "freezing" responses shown by some calves when separated from their mothers. The "bounding" act by the mother may inhibit the following response because of the intensity of the visual stimulus. This would explain why older calves no longer show the motionless response when the mother bounds away. On the other hand, in the case

of very young calves the mother's departure may be so rapid that the infant does not receive sufficient stimulus to elicit orientation and initiation of the following response.

The exploratory behavior described in Section 6 may be seen in some calves during their first day. Several recent workers have suggested that such behavior may be based upon the seeking of optimum levels of stimulation (see discussions by Rheingold and Gewirtz in Foss, 1961, for example). Little mention has been made of the importance of the above phenomenon in eliciting the activities that have been called "play" in infra-human mammals. Most of the activity that I have called "exploratory behavior" and "play" in caribou occurred at times when the level of stimuli directed towards the calves was relatively low. The events often followed nursing and the mother was almost always resting or feeding at the time. Exploratory behavior was not observed in traveling groups or in ones that were otherwise active or disturbed. The possible role of exploratory behavior in relation to the social responses of caribou has already been mentioned. The suggested importance of this role is in keeping with Leuba's theory that the seeking of optimal levels of stimulation is important to the learning process.

Altmann (1962) has suggested the importance of frequent, brief suckling periods in reinforcing the following response of caribou calves. It is possible that the frequent suckling of young calves may be of greater significance for the maintenance of this following response than it is for

nutritional reasons.

The frequency of nursing among sheep, which apparently have the highest frequency among domestic animals (Hafez, 1962), is somewhat below that of caribou, although the duration of each suckling event by young lambs is much longer. Munroe and Inkson (1957) have shown that lambs allowed to suckle only once every 4 hours obtained as much milk per day as those suckling every hour. The mother-infant relationships of caribou and sheep show many similarities in the frequency of contacts, both nursing and non-nursing, and in the development of a strong following response on the part of the infant, as well as in the fact that the infant is not normally "cached" while the mother feeds.

By their second day calves begin to show discrimination and recognition of their own mothers. Withdrawal to the mother following threats and orientation around the mother during exploratory activity are evident. But in spite of this ability to recognize the mother, approach and following responses are still made to any adequate form or movement stimulus. A calf several days old may immediately follow a human if the mother is not present. Escape (or avoidance) responses are weak, if present at all.

On four occasions when approach responses were made towards humans, the calves approached to within a few feet or until contact was made. Then, however, perception of the human odor (as shown by the distinct wrinkling of the nose) led to a halt or slight withdrawal. Approaching was renewed

when the human again moved slowly away. This alternate approach and withdrawal could be repeated several times. On two other occasions calves under one week old that kept running from the taggers even after separation from their mothers showed following responses after capture and handling.

There is little indication that the caribou calf is imprinted on its mother, at least in the classical sense of a relatively irreversible following response learned during a brief critical period. Instead there appears to be a gradual development of a "neuronal model" (Salzen, 1962) of the followed object. This development eventually leads to fear and escape responses towards stimuli not associated with the model. This "neuronal model" is clearly open to modification. Murie (1935) described how a caribou calf captured in September (3 months old) became "attached" to its owner in 10 days and showed a following response, bleating and searching for the human when he left.

Since in large aggregations it is impossible for the mother and infant to maintain close contact with each other at all times, it is advantageous for the infant to maintain its strong following response to relatively generalized stimuli at times of disturbance, rather than responding only to individual characteristics of its own mother. The continuing predominance of the following response over independent escape reactions in yearlings has already been described. In contrast to the importance of generalized stimuli

for calves, cows show many reactions which are given only, or most strongly, to stimuli from their own infants. During tagging operations cows were observed to reject strange calves immediately while searching for their own infants. In these cases the possible effects of a human odor on the strange calves cannot be excluded. However, at river crossings and in other natural situations where cows were temporarily separated from their infants, the cows paid little or no attention to strange calves. These same cows made immediate contact with their own calves, usually without hesitation or any overt uncertainty. Similarly, when groups were disturbed but the source of disturbance was not immediate, cows searched for their own calves and ignored other infants.

In Section 6 I described how some apparently deprived cows did attempt to lure calves away from their mothers. Therefore, there must be some conditions or some period after which deprived cows will accept a calf other than their own, but these conditions could not be determined in my study. Pruitt (1960) believes that successful adoption of lost calves is quite common but there is no evidence available to support this opinion.

A Comparison of Caribou Behavior with that of Wildebeest and Thomson's Gazelle.

Recently two detailed studies of African ungulates in their natural environment have been published, one on Thomson's gazelle by Brooks (1961) and one on the white-

bearded wildebeest by Talbot and Talbot (1963). In many ways these two tropical species are ecological equivalents to the barren-ground caribou. They are the major large herbivores and prey species of the East African grasslands, just as the caribou is on the tundra. All three are gregarious and migratory (although Talbot and Talbot do not consider the wildebeest to be truly migratory). It is of interest, then, to see what differences and similarities there are in the behavior of these three species, one of them an arctic cervid, the other two, tropical, bovid species. In Table 22 I have summarized some aspects of the behavior of these 3 species for comparison.

Perhaps the most important differences between the caribou and the two bovid species in these aspects of behavior are related to the great seasonal changes that occur in the habitat of the caribou at relatively fixed times every year and the resultant restriction of the breeding season. Although marked seasonal changes in precipitation occur in the East African grasslands, they are somewhat more variable in their annual timing. Moreover, the wildebeest and gazelle are in part able to compensate for the effects of the dry season by seeking localized refugia of green vegetation. Brooks considers it possible that the gazelles are also able to delay parturition until short dry periods pass. Along with the decreased importance of an exactly timed calving period there is evident a less restricted breeding season in the wildebeest and gazelle and a corresponding

Table 22 . A comparison of some aspects of behavior in the barren-

<u>Aspect of Behavior</u>	<u>Barren-Ground Caribou</u>
1. Length of migration	50 to 300 miles or more each way.
2. Calving grounds	Traditionally fixed.
3. Twins	None.
4. Calving season	Definite annual peak, May-June, 90% of calves born in 2 weeks or less.
5. Place of parturition	Cows rarely seek isolation, other individuals ignore neonate.
6. Post-partum behavior	Join groups within 5 hours after birth, if not already in one; groups usually predominantly cows and calves.
7. Concealment of young calves when disturbed	Erratic motionless behavior shown in first day or two, poss. elicited by "bounding" of cow away from calf.
8. Play by calves	Mainly lone exploratory activity, contacts between calves infrequent and brief.
9. Separation of cow and calf	Probably varies from 9 to 12 months, more female yearlings than males return to calving grounds.
10. Permeability of groups	Completely open.
11. Rutting groups	Harems rare and unstable, membership in groups constantly changing. One to many males in each group, no antagonism shown towards yearling males or adults not showing rutting behavior.
12. Territorial behavior	None evident.
13. Dominance hierarchy	No fixed hierarchy, dominance according to class and individual situation.
14. Reactions to humans	Poor recognition of motionless form, less wary in large groups, following response to abnormal objects weak in adults.
15. Alarm signals	Vocal, with special grunts by cows for calves. Alarm pose and alarm leap but no pilomotor signals. Olfactory alarm signal made by leaping on hind legs.

ground caribou, the white-bearded wildebeest and Thomson's gazelle.

<u>White-bearded Wildebeest</u> (Talbot and Talbot, 1963)	<u>Thomson's Gazelle</u> (Brooks, 1961)
1. 100 to 400 or more each way.	30 to 100 miles.
2. Variable, doubtful if any tradition involved.	Uncertain if tradition involved.
3. None.	None, but cows may give birth twice per year.
4. Born from late Nov. to early May, peak in Jan. and Feb. when forage conditions best.	May be born at all seasons, but two peaks corresponding with wet seasons.
5. Variable, female often in or near herd.	Females seek isolation.
6. Others may gather around neonate. Neonate up and running in 5 min.	Remain in cow groups for 2 to 3 months.
7. No motionless behavior by calf.	Show motionless concealment, cows obs. to nudge calves before leaving, make distracting movements.
8. Young calves butt and chase each other, occ. "spronking".	Frisking, gamboling, exploratory runs, mock fights.
9. Not until birth of next calf. Females may remain with calf after this.	At 8 months, males forced out of "harem herds".
10. Open, except breeding herds to adult males.	Open, except for adult males in "harems".
11. Temporary (few days) may be 2 or 3 adult males in each.	"Harem herds", dominated by 1 adult male, exist throughout year.
12. Temporary, moving territory around breeding herds.	Weak, but strongest among solitary males.
13. None observed.	Dominant male in each harem.
14. Pronounced following response, even in adults.	Poor recognition of motionless forms.
15. Vocal, special snort by mothers for calves.	Flicking of flank stripes, "spronking" (leaping in air), no vocal.

increase in the importance of male-centered social groups, although both Talbot and Talbot and Brooks note the temporary nature of these groups. Of course the possession of horns throughout the year would also tend to favor the greater role of males in the social organization of bovids. The "harem-type" grouping seems to be more developed as a year-round phenomenon in the Thomson's gazelle. The gazelle has a less restricted calving season than the wildebeest and in addition the females may be bred twice in one year.

McEwen (1963) notes that all three ungulates of the North American Arctic, the caribou, the musk ox (Ovibos moschatus), and the Dall sheep (Ovis dalli) normally produce only one young at a time. It may well be that the production of a single infant not only increases the chances for survival of the infant in Arctic species but is generally an adaptation of value to migratory ungulates.

As Talbot and Talbot describe, the wildebeest infant is far more precocious than either the caribou or the bison. They note that the wildebeest calf is more vulnerable to predators. There are a larger number of predators of several species preying on wildebeest calves. In addition, the distinct peak in caribou births and the concentration of calving animals in a limited area decreases the danger of predation on any one young caribou calf.

Of interest is the description by Talbot and Talbot of the attraction the neonate wildebeest calf has for cows and yearlings. These individuals gathered around the mother

and her infant and formed an island in the moving herd until the calf was able to travel. Marjoribanks Egerton (1962) describes a similar attraction to newborn American bison calves among enclosed animals. It is possible that such a behavior pattern could aid the survival of bovid calves born during migrations. The behavior would be of greater value in species in which the peak of calving was not pronounced or in which the timing of migratory movements was more variable. Similar behavior was not observed in caribou.

It may be seen in Table 22 that the wildebeest and Thomson's gazelle differ from one another in several aspects of behavior and in many of these aspects one of the two shows greater similarity to the caribou. Thus the behavior patterns of the nature considered in the table are not good indicators of the phylogenetic relationship between the wildebeest and Thomson's gazelle. The males of both the African species do show a complex of preliminary agonistic behavior common to many bovids. This behavior includes pawing at the ground, dropping to the knees of the forelegs (not mentioned by Brooks, 1961), rubbing the shoulders, head and horns on the ground, and shaking of the head. A similar series of events occurs in the agonistic behavior of the American bison (McHugh, 1958), the musk ox (Tener, 1954) and the Camargue cattle (Schloeth, 1958), among other bovids.

This complex of behavior is lacking in the agonistic behavior of the caribou and apparently in that of other cervids, although pawing appears in territorial marking by

roe deer (Hennig, 1962) and in the making of wallows by moose (Thompson, 1949).

It is interesting that pawing motions at the ground, so important in the winter feeding of caribou, do not occur in any social context in the species. During the rut the caribou male does thrash bushes with his antlers in a manner similar to the territorial marking of roe deer. In addition, both male and female caribou may rub the area around the base of the antlers and around the preorbital glands on saplings, usually beating the plant with their antlers at the same time. Hennig (1962) considers the homologous behavior in roe deer an olfactory marking of territories. What role these activities may play in caribou behavior remains uncertain.

SUMMARY

Some aspects of the behavior of the barren-ground caribou (Rangifer tarandus groenlandicus) were studied during four seasons in northwest Alaska. Particular emphasis was placed on the calving season and on mother-infant relationships.

The study population reaches maximum dispersion in the winter months at which time it is dispersed over more than 85,000 square miles. In contrast, during the postcalving migration at the end of June over 90 per cent of the population of approximately 175,000 animals may be found in one or two large masses. The migration of the population appears to make possible the most efficient utilization of the environment.

The calving area for the population lies in the foothills of the Arctic Slope of the Brooks Range in dry tundra dominated by Eriophorum tussock vegetation. Ninety per cent of the calves are born in 2 weeks at the end of May and in early June, although occasional late births occurred as late as the first week of July. Such abnormally timed births are more likely due to fertilization in a late estrous period rather than to variation in the length of gestation. The proportion of cows accompanied by calves at the end of the calving period was 73 per cent in 1960 and 42 per cent in 1961. Almost no adult males and only about 40 per cent of the yearlings enter the calving area. The calving ground is the most invariable point in the migratory pattern of caribou populations and appears to be traditionally determined.

Calving groups are entirely open and of a temporary nature but show both intra- and inter-group social facilitation. Coalescence of groups begins at the peak of calving and results in a constant increase in the size of groups until early July when a rapid process of dispersal begins. During calving, cows with calves tend to move together ("nursery bands") and yearlings tend to occur in groups with barren cows, but towards the end of calving all individuals, including adult males, are increasingly mixed together.

Cows may give birth while in groups or alone but usually do not actively seek isolation before parturition. Delivery is usually made from a standing position. The neonate stands within half an hour after birth and is walking soon after. The first nursing may be delayed until the second hour or later. If not already within a group, cows will attempt to join one within 4 to 5 hours after parturition. Stillbirths and other abnormalities associated with parturition were observed.

Until the processes of maturation and experience develop the calf to the point where it can survive independently, a strong following response as well as the mother's sense of identification with it are necessary for its survival. The mother provides the link between the calf and the rest of the caribou population by which the calf is able to synchronize itself with the population and participate in the population's movements until its own group responses develop. By the establishment of a strong bond between each mother and

her own infant, each calf is associated with a cow whose post-partum physiological and behavioral changes, such as the stage of lactation and the degree of sensitivity to unusual stimuli, are in proper synchrony with its own requirements for survival.

In the period immediately after birth the attraction of the cow and calf for one another appears to be based in great part on a positive responses towards increasing levels of stimulation. It has been postulated by Leuba (1955) that such responses facilitate rapid learning in mammals. Within a half-hour after birth the identification of the cow with her calf begins to develop. The infant, however, retains its following response to generalized stimuli. This response may be of value under conditions where groups are attacked by predators or otherwise disturbed so that the calf is separated from its own mother.

Since the infant is attracted to and shows a following response towards other caribou, the mother must maintain her bond with it by acts reinforcing the following response to herself: head bobbing, grunting, and attraction poses. In addition, agonistic acts are directed towards other cows, yearlings and strange calves that approach too close to her. If the cow and calf become separated after she has become sufficiently identified with it, she may show persistent searching behavior for at least 3 days after separation.

Head bobbing is a behavior pattern of widespread importance in the species. It is probably a displacement

activity derived from the feeding motion and occurs primarily in situations where the enacting individual is faced with a conflict of "drives". Ritualized head bobbing performed by cows is a strong releaser of approach responses in calves and shows qualities similar to experimentally produced stimuli eliciting such responses in young birds.

Other aspects of the calves' early behavior are considered as simple responses to stimuli of optimum intensity. Exploratory behavior is a common activity of young calves and may well be explained as a seeking of increased levels of stimulation. Its importance in learning is suggested. Social play is not developed in calves, that is, interactions between calves are infrequent and brief with no "games" observed.

Nursing is attempted either from the side or from between the hind legs. It is more often successful and of longer duration when performed from the side. The mean duration of each nursing (31 seconds) does not vary with age but the frequency (about once every 18 minutes in the first 2 days) decreases after the first week. Attempts by calves to nurse cows other than their own mothers and attempts by yearlings to nurse are frequently made but very rarely successful.

Five types of agonistic behavior occur. One ("antler threat") is directed primarily by cows towards calves. Outside of the rut, actual contact in agonistic events is rare, as are acts of reciprocation. The high degree of inter-individual tolerance is related to the nature of the early

social experiences of the calf. Cows with calves dominate other cows and all cows dominate yearlings. Cows without calves often show avoidance reactions when approached by calves, rather than agonistic behavior.

Sensitivity and responses to strange, disturbing stimuli vary greatly according to a variety of factors including the season and the nature of the group involved. Cows with calves show responses not shown by other individuals. If temporarily abandoned by their mother, infants may remain motionless when approached by a man but may also follow him after being handled.

Similarities are apparent in the behavior of caribou and their ecological equivalents of the African grasslands, the wildebeest and Thomson's gazelle. The more pronounced peak in breeding activity in caribou accounts for many of the differences.

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Addendum

* This publication, which had not been available in North America, was kindly sent to me by the author. Unfortunately, it arrived too late for consideration in the text.

The reference to the work of Semonov-Tyan-Shanskii in Flerov (1960) regarding antler retention is misleading. Semenov-Tyan-Shanskii actually cites the observations of Lapps that most bearing cows lost their antlers within 3 days after calving, however, he cites the observation of Palmer (1934) that reindeer cows retained their antlers 5 to 7 days post-partum. Semenov-Tyan-Shanskii also noted that all barren cows shed their antlers in March or April.

The data of Semenov-Tyan-Shanskii also show the strong tendency for yearlings and calves to occur in separate groups until the end of the calving period. However, the changes in the size of groups seen by him are quite different from those I observed. On the Kola Peninsula the largest aggregations (up to 300 head) were seen before calving and group sizes were minimal immediately after calving.

It is unfortunate that the excellent work of Semenov-Tyan-Shanskii with reindeer and moose has not received more attention from North American biologists.

APPENDIX A

Descriptive Notes for Scenes in the Film "The Behavior of the Barren Ground Caribou" Relating to the Calving and Postcalving Periods.

The scenes are numbered in their order of occurrence in the film. The underlined titles appear in the film. Figures in parentheses give the minutes and seconds between the end of the preceding title and the start of the event described.

The calving period

No. 1. A nursery band is shown moving through Eriophorum tussock vegetation in early June. The group is composed primarily of cows with young calves.

A nursery band

A few yearlings and barren cows trail along at the end of the nursery band.

Birth

No. 2. A cow giving birth is left alone on a ridge as the group she was with moves on by. She changes position 10 times during the 25 minute labor, rising and lying alternately and feeding sporadically. (1:20) The birth occurs. Fourteen minutes after the birth the mother crouches and passes fluid. Another female passes by a few feet away but pays no attention to the neonate. The calf has been attempting to rise again and the mother grunts to it. Eventually the pair

move slowly off in the same direction as all other caribou going by.

Another calf, two hours old, attempts to follow mother.

Head bobs elicit following.

No. 3. The mother is attempting to join a group of cows and calves out of sight towards the upper right corner of the picture. The calf is slow in developing and continues intermittent efforts to follow as shown for 2 hours. Head bobbing by the cow is more erratic than normal.

A calf under four hours old.

No. 4. The color of the calf blends in well with that of the withered, brown vegetation of the tundra. In this case the calf remained down when the mother left it, but is not perfectly motionless. When approached by the man head bobbing towards it, it rose and moved away slowly. Other calves responded by approaching the man under similar circumstances.

Nursing is at first most often from the side, later more often from the rear.

No. 5. A calf follows its mother closely, attempting to nurse whenever she stops to feed.

Solitary play - Exploratory -

No. 6. A lone calf, whose mother is not within a nursery band, makes exploratory runs in "figure 8" patterns around its mother. The mother is feeding and moving intermittently. Occasionally a mother will notice the movements of her calf and chase it, attracting its attention, as this cow starts to do here.

Calf recognizes and responds to own mother's call.

No. 7. Several events were observed that indicated a calf learns to recognize its own mother's call and may not react to that of another cow, even though this cow's infant does so from nearby. Here, the calf goes to nurse after returning to its mother, but bunts so vigorously that the mother backs away.

Calf attempts to suckle wrong cow, returns to mother.

No. 8. A calf moves ahead of its feeding mother, approaches another cow and attempts to nurse. This cow makes no aggressive action but moves away quickly. The calf (2 or 3 days old) then returns to its mother.

Play

No. 9. One calf approaches another with gamboling movements. The other immediately moves away. A typical calf-calf interaction.

Play is only occasionally seen in older animals.

No. 10. Filmed in mid-November. A calf and a yearling engage in a long bout of play, with mock battles, attempted mounting, and chasing. Action continued for one-half hour. The younger animal was the most active and the instigator of each event. (0:40) Two excitation leaps are made by the calf in play fleeing.

Fright Reactions - a true "excitation leap"

No. 11. A yearling, frightened by the photographer, gives a complete excitation leap before fleeing.

Other fright reactions

No. 12. The head bob (0:05 and 0:18), indicative of uncertainty in disturbed individual. Exaggerated flight (0:10-15). The tail is raised and the gait is "bouncy".

No. 13. Urination pose (0:25). One hind leg is extended diagonally outward to the side while the animal faces the source of alarm.

No. 14. The agonistic behavior in this scene is all stimulated by the presence of an earth lick. (0:30, 1:15 and 1:35) slight "antler threat" gestures. (1:35 and 1:50)

Rearing. In the first event both cows rear up, in the second the recipient of the threat back away without reciprocating.

(0:55) Calf attempts mounting act on own mother.

(2:00) Mother starts to make antler-threat towards own calf.

The throng

No. 15. A large postcalving aggregation in the first week of July was filmed on the north slope of the De Long Mountains. About 20,000 animals were in sight at the time the scene was filmed. Although the individuals are spread out, they appeared as one continuous mass when viewed from high altitude.

No. 16. In a closer view of a more dense postcalving aggregation, a calf, between 1 and 2 weeks old, has been separated from its mother and stands head bobbing. The mother is searching for it, grunting continually. The two are reunited and both start grazing. It is characteristic of calves of this age to graze with their heads very close to their mothers' heads.

Cow - calf separations during migration

No. 17. A calf, perhaps 2 weeks old, travels alone, and pays no attention to the other individuals. Its mother searches for it, moving from left to right, counter to the direction of migration. When the two meet the calf goes directly to nurse with no preliminary muzzle to muzzle contact or head bobbing as often occurs.

Separations most often occur at river crossings

No. 18. A cow returns across the river (from right to left) looking for her calf. She disregards other calves separated from their mothers.

No. 19. A calf refuses to follow its mother across (at right side of frame) and returns up the bank. Then the same calf crosses at the left. Another cow is seen coming back to locate her calf.

No. 20. A calf over two weeks old was found with its dead mother. The calf grazed a little and frequently attempted to nurse from the carcass. It showed little fear of humans, but no following response. When it received the human odor at a distance of a few feet it withdrew slightly.

Summer

No. 21. By mid-July the large aggregations are beginning to break up into distinct, compact, but still open, groups. Here one such group is seen resting on aufeis (remains of overflow and snow frozen together that may be present on river beds well into late summer). Aufeis and isolated snow patches attract groups and are used for midday resting.

No. 22. Browse is of importance during a limited period in July when the high willows along the rivers are used. The rapid changes occurring in the pelages of most individuals at this time are noticeable.

Reactions to insects

No. 23. The annoyance caused by insects decreased the wariness of these caribou. Note the vigorous exhaling movements and the twitching of the skin on the back. One individual, however, does note the photographer standing in open sight on the tundra and gives an alarm pose (0:38).

August

No. 24. During August most of the population is dispersed on the tundra and broken up into small bands. The dark summer pelages make the animals far less conspicuous at this time of year.

APPENDIX B

Table 1. Weather conditions - northwest Alaska calving grounds

May 16 - June 27, 1961.

Location and Date	Temperature		Wind (m.p.h.)	Precipitation Cl.= cloudy	Approximate Wind chill*
	Min.	Max. (F.)			
Elusive Cr., Utukok R.					
May 16	20	34	N 5-8	Cl.	900
17	18	27	N 7-10	Cl.	
18	20	50	N 5-12	Low Cl., lt. snow	1,000
19	24	30	N 3-6	Low Cl., drizzle-snow	850
20	16	32	N 0-6	Cl., snow-flakes in AM	850
21	12	40	E-N under 2	Clear	700
22	22	39	NE 10-12	"	1,000
23	24	44	NE 8-12	"	1,000
24	22	45	NE 10-16	"	1,000
25	30	65	NE 5-9	"	800
26	38	52	SW under 3	Lt. rain	550
27	32	56	SW-NW under 3	Fog and rain	600
28	29	55	SW-NW under 3	Rain, early AM	650
29	30	44	NW-N 3-9	Rain	800
30	30	44	NE-E 10	Lt. rain	900
31	33	50	E-NE 4-10	Fog in evening	750
Avalik R.					
June 2	32	54	N-W 3	Cl., lt. rain in PM	700
3	33	62	E-N 3-7	Clearing	700
4	26	56	E-N 3-10	Clear	900
5	30	50	E-NE 8-16	Drizzle	900
6	43 at 0900		NE 10-16	Rain in PM	700
7	43 at 0830		S 7-9	Fog and rain	650
8					
9		60	N under 10		
10					
11					
12	32	54	N 7		800
13	40	54	NE 5	Cl.	650
14	42	58	N under 3	Rain	450
15	43	52	S 3	Cl.	550
16	44	60	S 5-9	Rain	600
17	?	?	SE 26-40	Cl.	750 (?)
18	40	70	SE 10-14	Rain	750
19	35	60	S under 5	Fog	650
20	32	44	S 5-8	Snow	800
21	28	38+	N 7	Snow	850

* Based on minimum temperature and average wind velocity.

APPENDIX B

TABLE 2

Weather Records, 1962
Precalving and Calving Periods, Elusive Creek, Utukok River Alaska

<u>Date</u>	<u>Temp. (F.)</u>			<u>Precipitation</u>	<u>Approximate</u>
	<u>Min.</u>	<u>Max.</u>	<u>Wind</u>	<u>Cl. = cloudy</u>	<u>Wind Chill*</u>
<u>May</u>					
22	27	47	S 5-10	sunny	900
23	23	45	S 5-10	sunny	950
24	28	41	N 15-20 calm in evening	Cl., lt. rain in PM	950
25	29	50	N 5-10 occ. gusts 15-20	Cl.	950
26	30	38	N 5-10	Cl. snow squalls	850
27	29	33	N 8-10	Cl. snowing	900
28	24	31	N-NE under 5	Cl., snow and hail	750
29	21	42	NE 5	clear, sunny	900
30	29	52	NE 5-10, occ. gusts to 15	part Cl.	900
31	30	50	E 12-15	AM sunny, PM Cl.	900
<u>June</u>					
1	31	58	N-NE 10-15 calm in evening	Cl.	900
2	33	--	N-NE under 5	Cl., lt. rain	600
3	31	33	NW 5-10, gusts to 15	snow-ceiling, zero	900
4	30	38	NE 12-15	snow and sleet	950
5	24	34	N 10-14, gusts to 20, even. under 5	occ. snow squalls	1000
6	27	45	SW AM calm, PM 12- 15, even. under 5	snow squalls in morn. and even.	950
7	32	46	N-E 5-10 calm in evening	snow flurries	800
8	32	60	S under 5	sunny	600
9	43	66	SW under 5	Cl., night rain	500
10	44	66	SSW 6-10	AM sun. PM Cl. 1 rain shower	600
11	43	--	----	Cl.	---
12	--	68	----	Cl.	---
13	47	--	----	Cl., rain	---
14	39	67	AM NW 10-12 PM under 3	sunny	700
15	35	66	W 10-15, night calm	Cl.	500
16	37	68	N-NE under 5	sunny	550
17	42	76	AM SW 7-12, PM W under 5	part Cl. 1 rain shower	600
18	39	73	AM W 5-8 PM under 5	clearing in PM	650
19	54	70	SW 15 gusts to 22 in PM	PM Cl. and rain	550

* During night. Based upon minimum temperature and average wind velocity.

APPENDIX C

Table 1. Number of cows with antlers, cows without antlers and yearlings in 40 groups observed in the central area, May 22 to May 29, 1961.

Antlered Cows (w/a)	Unantlered Cows (wo/a)	Yearlings (Y)	Antlered Cows	Unantlered Cows	Yearlings
22	1	4	13	1	1
26	5	7	27	2	2
20	3	5	8	1	0
4	2	2	5	1	1
36	4	4	19	0	1
6	1	1	3	0	0
8	2	5	12	2	2
7	1	1	10	2	1
11	2	1	16	3	1
5	3	1	6	3	2
0	2	2	39	10	3
2	1	0	67	11	6
16	4	6	5	0	2
15	2	3	55	9	8
5	3	1	49	10	5
5	3	1	17	3	5
13	4	1	16	7	1
60	21	24	8	5	3
8	6	5	21	6	3
18	1	3	17	4	2

Correlation coefficient between (wo/a) and (Y) = .87, $Z_1=2.67$

Correlation coefficient between (wo/a) + (w/a) and (Y) = .69, $Z_2=1.69$

Test of significance of difference between Z_1 and Z_2 shows the standardized normal deviate = 4.18, therefore $P < .01$.

APPENDIX D

Analyses of Caribou and Reindeer Milk

Table 1. Analyses of caribou milk specimens from cows
collected during their first month of lactation.
(per cent by weight)

Coll. No.	Total Solids	Fat	Protein		Lactose	Ash	pH	
			Casein	Whey				
HK 44	25.4	13.0	6.2	1.2	7.4	3.1	1.3	6.50
HK 52	22.6	10.6	5.6	1.5	7.1	3.2	1.4	6.44
HK 51	24.2	11.4	7.3	1.4	8.7	4.6	1.2	6.44

Minor constituents - per cent by weight

	Non-protein Nitrogen	Calcium	Phosphorus
HK 44	0.10	---	---
HK 52	0.15	0.29	0.18
HK 51	0.10	0.34	0.22

APPENDIX D (continued):

Table 2. Analyses of reindeer milk.

Source	Total solids	Fat	Crude Protein*	Lactose	Ash
Barthel and Bergmann, 1913	36.7	22.5	10.3	2.5	1.4
Gulchak, 1954	35.75	19.73	--	2.61	1.48
Aschaffenburg et al., 1962		early in lactation period			
		9.2	7.22	3.87	
		late in lactation period			
		16.96	11.46	2.75	
Berge, 1963		early in lactation period			
		15.1	8.7		
		late in lactation period			
		24.7	11.5		

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